A SYSTEMATIC STUDY OF *ASTER* SECTION *PATENTES* (ASTERACEAE)

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ABSTRACT

Aster section *Patentes* is a group of base-5 asters of the eastern United States. The group is characterized by widely-spaced, strongly-clasping cauline leaves, abruptly-reduced peduncular bracts, and glandular, green-tipped phyllaries. Three species are recognized in the section: *Aster phlogifolius* Muhl. ex Willd., a tetraploid, Appalachian taxon; *Aster georgianus* Alexander, a decaploid, Piedmont taxon; and *Aster patens* Ait., a wide-ranging taxon including both diploid and tetaploid populations, and divisible into three geographic varieties—the southwestern var. *gracilis* Hook., the Interior Highland var. *patentissimus* (Lindl.) T. & G., and the eastern var. *patens*. The results of historical, morphological, chromosomal, hybridization, and ecological studies are presented, and the taxa are keyed, described, mapped, and synonymies are given.

INTRODUCTION

The taxa centered around *Aster patens* Ait., were grouped as section *Patentes* of the subgenus *Aster* in Torrey and Gray's *Flora of North America* (1841). This group of taxa, here divided into three species, has been subjected to various treatments, being segregated into six species in some treatments (Burgess in Small, 1903; Alexander in Small, 1933), and grouped into a single species, *Aster patens*, in others (Torrey and Gray, 1841; Gray, 1884; Fernald, 1950; Gleason and Conquist, 1963; and Cronquist, 1980). The synonomy of the group involves 22 names.

This paper represents the first effort at a systematic study of *Aster patens* and related taxa. A part of the study was done to gain an understanding of the affinities of the group to other asters. Therefore, included in this paper, are correlative studies, observations, and comments on other base-5 asters, especially the section *Grandiflori*. Special attention is given to the resemblance and possible relationships between *Aster georgianus* Alexander and *Aster grandiflorus* L.

MATERIALS AND METHODS

This study is based primarily on field familiarity with the plants, gained from visits to over 100 populations in 14 states. Transplants representing all taxa were grown at a garden in northwest Davidson County on a rich creek-botton site in full sunlight for 2–4 years. Additional transplants were maintained at the Vanderbilt University garden and greenhouse. Seedlings

SIDA 10(1): 41–81. 1983.

representing all taxa were raised to maturity in a potting soil mixture in the greenhouse and observed for 1–2 years. Voucher specimens from garden and greenhouse plants are housed at VDB.

A total of 3104 specimens from 32 herbaria were examined during this study. A citation list of these specimens is available upon request. All of these specimens were subjected to a detailed qualitative and quantitative analysis, including surveys of habit (slender rhizomes vs. caudices), leaf length and width, phyllary tip length (green portion), phyllary pubescence and width, and involucral height. These data were then used to prepare a series of maps, histograms, and scatter diagrams (R. Jones, 1980).

Population samples were also gathered (15–20 specimens per population, 5 populations per taxon), and used to prepare additional tables for comparisons of morphological features, including guard cells and pollen grains.

Seedling root tips from germinating achenes were used to obtain chromosome counts. In most instances achenes germinated readily at room temperature on moist filter paper in a petri dish (achenes of *Aster phlogifolius* require a cold treatment for good germination). The Fuelgen techniques, with pretreatment in 0.03% 8-hydroxyquinolin, was used to make the counts. Slides were made permanent by the dry-ice freeze method, and documented by photographs and camera-lucida drawings.

In hybridization studies, the crosses were accomplished by rubbing together the flowering heads of different individuals. Heads were bagged before and after crossing to prevent contamination. About a month later the heads were harvested and percentage seed set determined; each head was considered as a single crossing attempt.

TAXONOMIC HISTORY

The taxonomic history of *Aster* section *Patentes* began in 1789 with the original description of *Aster patens* in William Aiton's *Hortus Kewensis*. Gray (1882) states that Solander was the actual founder of the asters in *Hortus Kewensis*, and Krok (1925) lists *Aster patens* as a name attributable to Dryander. Aiton is cited as the official author of *Aster patens*, however, because neither Dryander or Solander were acknowledged in the work.

According to the type citation, the specimen (BM) that provided the basis for the original description of *Aster patens* was a "native of Virginia, introduced about 1773 by George Ausrere, Esq." This specimen was collected from the Chelsea Physic Garden, and is a part of the Philip Miller herbarium. Miller was evidently not the actual collector of the cultivated specimen, because the introduction date of 1773 was two years after his death.

The specific epithet *patens* referred to the spreading, elongate branches; this species was characterized further in its type description by the roughly-pubescent stems, the oblong, entire, acute, cordate-clasping and scabrous leaves, and the imbricate, slightly recurved phyllaries. Since its original publi-

cation, *Aster patens* has been widely accepted as a distinct species of the eastern United States.

Willdenow (1803) described *Aster phlogifolius* from a specimen (B) collected by Muhlenberg in Pennsylvania. The specific epithet referred to the phlox-like leaves, which were described as lanceolate, entire, cordate-amplexicaul, and softly pubescent. The original description also referred to the pubescent, unbranched, and apically-panicled stems, and the loosely imbricated and lanceolate phyllaries. This Willdenow taxon was reduced to a variety of *Aster patens* by Nees (1832); most subsequent authors, including Cronquist (1980) and A. Jones (1980b), have followed this judgment. In this treatment, however, I have accepted *A. phlogifolius* as a species distinct from *A. patens.*

In the early part of the 19th century many authors confused *Aster patens* and *A. phlogifolius* with *A. undulatus* L., *A. diversifolius* Michx., and *A. amplexicaulis* Michx. (*non* Lam., *nec* Muhl. ex Willd.). This confusion was clarified by Gray (1882, 1884), who stated that *A. amplexicaulis* Michx. was *A. patens* Ait., and that *A diversifolius* Michx. belonged with *A. undulatus* L. My determinations from type material of the Michaux and Linnaean taxa are in accord with those of Gray.

Aster patens var. *gracilis* was described by Hooker (1835) from specimens (K!) collected by Drummond near Jacksonville, Louisiana, in 1832. This varietal epithet applies to the slender habit of the plants, noteworthy for their long branches and small leaves. It should be noted that the Jacksonville referred to by Hooker was in Louisiana and not in Florida as stated by Mohr (1901). Current maps do not indicate a Jacksonville for Louisiana, but Tanner (1844) shows a Jacksonville in Washington Parish, just east of Franklinton, on the Bogue Luse River, near the present town of Sheridan.

Drummond was also the collector of the type specimen of another currently recognized variety—*Aster patens* var. *patentissiumus*. This specimen (CGE!) was collected in the vicinity of St. Louis, Missouri in 1831. Lindley (1836) distinguished *A. patentissimus* from *A. patens* by its very spreading branches, its short-peduncled, turbinate heads, and by its wooly obtuse phyllaries. In the type citation, the distribution is given as "Louisiana," but the type specimen is clearly labeled "Saint Louis." This taxon is here treated in the sense of Torrey and Gray (1841), as a geographic variety of *A. patens.*

As originally conceived by Torrey and Gray (1841), the section *Patentes* consisted of a single species—*Aster patens*, with three varieties—*gracilis*, *phlogifolius*, and *patentissimus*. In this first treatment, the section was defined by the rather large heads, with turbinate to campanulate involucres, the closely imbricated phyllaries with spreading tips, the silky-canescent achenes, the cordate-clasping, entire, pubescent or scabrous cauline leaves, and the much smaller leaves of the branchlets (the glandular pubescence of the phyllaries was not mentioned). Included in the synonymy of the group are *A. auritus* Lindley listed under var. *phlogifolius*, and *A. arnottii* Nees ex

T. & G., listed under var. *patentissimus*. After examining type material from these Lindley and Nees taxa, I concur with Gray's placement of these names.

Other names to be placed into the synonymy of var. *patentissimus* are *Aster continuus* Small (1898), and *A. subsessilis* Burgess in Small (1903). Mohr (1901) renamed *A. patens* var. *gracilis* as *A. patens* (var.) *tenuicaulis*, and Burgess in Small (1903) elevated this taxon to the rank of species as *A. tenuicaulis*.

Alexander described two new species in the section *Patentes* from Small's Manual (1933)—*Aster fontinalis* and *A. georgianus*. *Aster fontinalis* was based on a specimen (NY!) collected by Small near Deep Lake, in southern Florida, in 1925. This species was characterized by the linear-elliptic and auriculate-clasping leaves and by the thinly-linear phyllaries. Long (1970) listed *A. fontinalis* as a synonym for his new variety *A. patens* var. *floridanus*, based on a specimen (GH!) collected by Brass from Collier County, Florida, in 1945. As a result of a study of these types and specimens collected during this investigation (*R. Jones 1272*), I have excluded these taxa from *Aster* section *Patentes*. Cronquist (1980) allies *A. fontinalis* with *A. dumosus* L.

Aster georgianus was based on a specimen (NY!) collected by Cuthbert near Augusta, Georgia, in 1898. Alexander delimited this Georgia aster from *A. patens* by its fewer branches, thicker leaves, and larger heads. This taxon met with little acceptance until 1977 when Cronquist proposed varietal status under *A. patens*. *Aster georgianus* is maintained in this revision as one of the three distinct species in *Aster* section *Patentes*.

Published names associated with *Aster patens* and not previously discussed include: *A. patens* Ait. f. *rosea* Svenson (1936), a pink-liguled form of *A. patens*; and *A. patens* var. *patens*, validated by Cronquist in 1947 as the typical variety of the species.

Semple and Brouillet (1980a,b) placed *Aster patens* along with other base-5 asters in the genus *Lasallea* Greene; all of these taxa were then transferred for reasons of priority to the genus *Virgulus* Raf. by Reveal and Keener (1981). These nomenclatural changes have resulted in the publication of six new combinations related to *A. patens*, and a total of 40 new combinations related to base-5 asters.

SECTIONAL LIMITS AND RELATIONSHIPS

The evolution and classification of the chromosome groups in *Aster* based on $x = 5$, 8, and 9 are the subjects of recent publications and considerable disagreement. I would agree that the base-5 asters constitute a distinct phylogenetic grouping, but I have classified them as a subgenus, for reasons cited by A. Jones (1980a), rather than as a separate genus, as proposed by Semple & Brouillet (1980a), and followed by Reveal and Keener (1981).

According to the classification of A. Jones (1980a), the subgenus *Virgulus* includes six sections of base-5 asters, one of which is the section *Patentes*.

The section *Patentes* is expanded to include the southeastern *Aster walteri* Alexander in Small, and *A. adnatus* Nutt., the Bahaman *A. lucayanus* Britt., and the Central American taxa centered around *A. moranensis* H.B.K. These taxa, however, possess features that set them apart from *A. patens, A. georgianus*, and *A. phlogifolius*. Both *A. walteri* and *A. adnatus* have numerous, tiny, bract-like leaves and hispidulous pubescence. *A. lucayanus* has sessile, oblanceolate leaves and sericeus pubescence, and *A. moranensis* has sessile, linear-oblong leaves and pilose pubescence. I have thus excluded these taxa from the section, and included in my study only those taxa that are clearly allied with *A. patens.*

Other species of the United States that are close relatives of *Aster patens*, but are traditionally placed in different sections, include *A. grandiflorus* L., *A. novae-angliae* L., *A. oblongifolius* Nutt., and *A. carolinianus* Walt. As a group, these taxa differ from the *Patentes* by the more crowded leaves, usually over 30 below the inflorescence, the leaves more linear-elliptic and only sessile to auriculate, and the penduncular bracts only gradually reduced from the upper cauline leaves. Because of its vine-like habit and glabrous achenes, *A. carolinianus* stands out as a distinct section (*Sagittiferi* Gray), but the relationships of the other three species are less clear (see A. Jones, 1980a; Semple & Broillet, 1980a). These three species are here referred to as the section *Grandiflori* T. & G.

CHROMOSOME NUMBERS AND KARYOTYPES

Prior to this study haploid chromosome numbers of 5, 9, 10, and 20 had been published for *Aster patens*, but numbers for *A. phlogifolius* and *A. georgianus* were unknown. For this study mitotic chromosome counts from 45 populations of *Aster* section *Patentes* were determined. For number and karyotype comparisons with the section *Grandiflori*, counts were also made from two populations of *A. grandiflorus*, one of *A. oblongifolius*, and one of *A. novae-angliae.*

The results of the chromosome number studies are listed in Table 1. All of the taxa investigated have chromosome numbers based on $x=5$. These counts confirm the existence of two ploidy levels in *A. patens*, at $2n=10$ and $2n=20$, and provide the first evidence of accessory chromosome in these populations. Original counts are presented for *A. phlogifolius* ($2n=20$), *A. georgianus* ($2n=50$), and *A. grandiflorus* ($2n=60$). These first reports have already appeared in publication (R. Jones and A. Jones, 1979).

ASTER PATENS var. PATENS. Prior tetraploid counts for the species have been reported by Huziwara (1941) from an unknown locality, by Avers (1954) from Indiana, and by Van Faasen and Sterk (1974) from New Jersey. A. Jones (1980b) reported tetraploids from Illinois and Kentucky, and Semple and Brouillet (1980b) have made counts of $2n=20$ from populations in Kentucky, Massachusetts, Mississippi, Missouri, and North Carolina. The listing of the number 20 as a haploid count by Huziwara (1958)

TABLE 1

CHROMOSOME NUMBERS IN ASTER

2n Number	Taxon, Locality, *R. Jones* Collection Number
	ASTER PATENS var. PATENS
20	ALABAMA. Barbour Co.: Eufaula. *2147.*
20	ALABAMA. Etowah Co.: Atalla. *2089.*
20	ALABAMA. Lee Co.: Phenix City. *2153.*
20	ALABAMA. Marengo Co.: Demopolis. *2142.*
20	ALABAMA. St. Clair Co.: Asheville. *2227.*
20	ALABAMA. St. Clair Co.: Asheville. *2229.*
10	ALABAMA. Sumter Co.: Epes. *2141.*
10 + 2B	ALABAMA. Sumter Co.: Gainesville. *2123.*
20	ALABAMA. Tuscaloosa Co.: Kellerman. *2121.*
20	FLORIDA. Leon Co.: Tallahassee. *810.*
20	GEORGIA. Rockdale Co.: Conyers. *2104.*
20	KENTUCKY. Carlisle Co.: Wickliffe. *2044.*
20	NORTH CAROLINA. Mitchell Co.: Spruce Pine. *1751.*
20	TENNESSEE. Cheatham Co.: Ashland City. *1728.*
20	TENNESSEE. Dickson Co.: Charlotte. *1230.*
20	SOUTH CAROLINA. Charleston Co.: Charleston. *2239.*
	ASTER PATENS var. PATENTISSIMUS
20 + 1B	ARKANSAS. Drew Co.: Monticello. *1954.*
20 + 0–4B	MISSOURI. Butler Co.: Popular Bluff. *2052.*
20	MISSOURI. Butler Co.: Popular Bluff. *2056.*
20	MISSOURI. Taney Co.: Forsyth. *2064.*
	ASTER PATENS var. GRACILIS
10 + 1B	ALABAMA. Sumter Co.: Livingston. *2130.*
10 + 1–2B	ALABAMA. Sumter Co.: Livingston. *2216.*
10	ALABAMA. Sumter Co.: York. *2217.*
20	LOUISIANA. St. Helena Par.: Greenburg. *2261.*
20	LOUISIANA. Tangipahoa Par.: Greenburg. *2265.*
20	LOUISIANA. Washington Par.: Bogaloosa. *2266.*
10	MISSISSIPPI. Kemper Co.: Scooba. *2218.*
10	MISSISSIPPI. Noxubee Co.: Shuqualak *2215.*
10	MISSISSIPPI. Oktibbeha Co.: Starkville. *2213.*
10	OKLAHOMA. Osage Co.: Bartlesville. *2069.*
10	TEXAS. Anderson Co.: Bushy Creek. *2253.*
20	TEXAS. Bowie Co.: Hooks. *2249.*
10	TEXAS. Houston Co.: Latexo. *2255.*
10	TEXAS. Tyler Co.: Colemeil. *2259.*
10	TEXAS. Walker Co.: Huntsville. *2258.*
10	TEXAS. Van Zandt Co.: Mineola. *2251.*
	ASTER PHLOGIFOLIUS
20	KENTUCKY. Powell Co.: Nada Tunnel. *2038.*
20	TENNESSEE. Grainger Co.: Thornhill. *2029.*
20	TENNESSEE. Grundy Co.: Palmer. *1987.*

ASTER GEORGIANUS

50	ALABAMA. Etowah Co.: Atalla. *2225.*
50	ALABAMA. St. Clair Co.: Asheville. *2098.*
50	ALABAMA. St. Clair Co.: Asheville. *2226.*
50	NORTH CAROLINA. Montgomery Co.: Troy. *2235.*
50	NORTH CAROLINA. Union Co.: Monroe. *2233.*
50	SOUTH CAROLINA. Cherokee Co.: Blacksburg. *2231.*

ASTER GRANDIFLORUS

60 + 0–3B	NORTH CAROLINA. Montegomery Co.: Troy. *2114.*
60 + B's	NORTH CAROLINA. Richmond Co.: Ellerbe. *2238.*

ASTER NOVAE-ANGLIAE

10	ALABAMA. Greene Co.: Eutaw. *1662.*

ASTER OBLONGIFOLIUS

10	TENNESSEE. Cheatham Co.: Ashland City. *2277.*

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was evidently a misprint, because the number was based on his 1941 count of $2n=20$. These counts together with mine suggest that populations of *A. patens* in the eastern United States are exclusively tetraploid, and that diploid plants are encountered only in the southwestern portion of the range of the species.

ASTER PATENS var. PATENTISSIMUS. Accessory chromosomes were noted in tetraploid counts from two populations of this Interior Highland taxon. Anderson et al. (1974) reported an aberrant number of $n=9$.

ASTER PATENS var. GRACILIS. The first diploid count for the species was reported by S. Jones (1968), from a population in Sumter County, Alabama. In recent publications the diploid number has been reported from Baldwin County, Alabama (Semple and Brouillet, 1980b), and from Natchitoches Parish, Louisiana, Lafayette County, Mississippi, and Smith County, Texas (A. Jones, 1980b). The distribution of diploid populations of *A. patens* therefore appears to range from western Alabama to Texas and Oklahoma. Tetraploid plants, however, occur over the entire range of the species. The three populations sampled from the vicinity of the original Drummond collections (*R. Jones 2261, 2265, 2266*) all yielded the tetraploid count.

ASTER PHLOGIFOLIUS. The tetraploid number of $2n=20$ was confirmed in three populations of this Appalachian taxon. A count of $2n=10_{II}$ was recently published by A. Jones (1980b).

ASTER GEORGIANUS. These decaploid counts from six populations of *A. georgianus* represent the first reports of a chromosome number of 50 among base-5 asters (chromosome numbers of 50 in the base-8 asters are the result of aneuploidy, rather than euploidy). Semple and Brouillet (1980b) also reported a count of $2n=50$ from plants they called *A. patens* in Richland County, South Carolina.

ASTER GRANDIFLORUS. In two populations of this large-headed aster, I found the surprising number of $2n=60$ + B's. A. Jones (1980b) has confirmed this number, publishing a meiotic count of $2n=30_{II}$ from plants that I collected in Montgomery County, North Carolina. This is the first report of a $2n$ number of 60 in the entire genus, and is the highest ploidy level so far determined for a base-5 aster.

ASTER NOVAE-ANGLIAE. The count of $2n=10$ agrees with that reported by many other workers, including Delisle (1937), Huziwara (1941) and Harriman (1978). Avers (1954) reported a tetraploid count.

ASTER OBLONGIFOLIUS. The diploid count was also reported by Stucky and Jackson (1975), but Smith (1965) reported a tetraploid count for plants from Arkansas. Semple and Brouillet (1980b) have obtained the tetraploid count for plants from Missouri, while A. Jones (1980b) reported the diploid count from New Mexico and the tetraploid from Illinois.

KARYOTYPES. As shown in Figure 1, the karyotypes of all the taxa investigated are based on the following haploid chromosome set: two short submetacentrics, about 2.0 and 2.2 μm long; one intermediate-sized acrocentric, about 3.0 μm long; and two longer acrocentrics, about 3.5 and 4.0 μm long. These five kinds of chromosomes are in duplicate in diploid *A. patens*, *A. novae-angliae*, and *A. oblongifolius*, and in quadruplicate in tetraploid *A. patens* and *A. phlogifolius*. The karyotypes of the high-polyploid species are more difficult to analyze, but the better spreads reveal that 20 of the 50 chromosomes of *A. georgianus*, and 24 of the 60 chromosomes of *A. grandiflorus*, are short submetacentrics. These are the numbers expected, assuming that these karyotypes are decaploid and dodecaploid multiples of the base-5 chromosome morphology.

In investigations of other base-5 species (Huziwara, 1958; Semple, 1976) a similar pattern can be identified. These studies also show, however, that there are differences in absolute chromosome size and in the visibility of secondary constrictions. Recently, Semple and Brouillet (1980b) also have noted this basic karyotype similarity among base-5 asters, and have found that the group is further set apart from other asters by differences in satellite chromosome morphology.

These considerations thus support the concept of a fundamental similarity of karyotype among base-5 asters. The simplest explanation of a similarity in chromosome number and morphology is a monophyletic origin of base-5 *Aster*.

MORPHOLOGY

These comments on the morphology of *Aster* section *Patentes* are based on observations and studies of plants in populations, in the garden and greenhouse, and as herbarium specimens. Interpretations of the relative significance of morphological features are based on the constancy of characters in the field and on their persistence in transplants and seedlings.

Figure 1. Chromosome numbers and karyotypes in *Aster* section *Patentes* and section *Grandiflori*. A. *Aster patens* var. *gracilis*—$2n=10 + 1$ B, B. *Aster oblongifolius*—$2n=10$, C. *Aster novae-angliae*—$2n=10$, D. *Aster patens* var. *patens*—$2n=20$, E. *Aster patens* var. *patentissimus*—$2n=20 + 1$ B, F. *Aster phlogifolius*—$2n=20$, G. *Aster georgianus*—$2n=50$, H. *Aster grandiflorus*—$2n=60 + 3$ B, I. Ideogram of base-5 *Aster* karyotype. The B-chromosomes are indicated by arrows.

Those characters that have proven useful in identification of the taxa are presented here within the framework of a discussion of the general morphology of the section.

HABIT. In mixed populations of *A. georgianus* and *A. patens* one of the most obvious differences between the two taxa is the growth habit. *Aster georgianus* is a colonial species—plants produce an extensive system of elongate rhizomes and the aerial stems arise singly, while *A. patens* is a cespitose species—the plants produce caudices and the stems arise in clusters. *Aster patens* will occasionally, especially in the sandy habits of the Coastal Plain, develop short rhizomes from the caudices, but these diploids and tetraploids still do not approach the spreading-colonial habit of the decaploid *A. georgianus*.

A. Jones (1978a,b) has discussed the habit of perennial asters and noted that these features are often genetically fixed and useful in diagnosing taxa. My garden studies suggest that the same observations apply to the *Patentes* —transplants of *A. patens* remain cespitose in the garden, while transplants of *A. georgianus* maintain their colonial habit. Plants of *A. phlogifolius* show no tendencies to be colonial in either the field or the garden; these plants produce a caudex, often with only a single, arching stem, or, in sunny habitats, they may be cespitose.

TRICHOMES. The trichomes of *Aster* section *Patentes* are very similar to those reported by Nesom (1976, 1978) from the related genera *Erigeron* and *Machaeranthera*. The indument formed by the large uniseriate, tapering trichomes on the stems and leaves varies from scabrous in *A. patens* and *A. georgianus* to soft-pubescent in *A. phlogifolius*. Smaller uniseriate trichomes occur on the phyllaries, the density varying with the taxon, being almost absent from the glabrate phyllaries of *A. phlogifolius*, and most prominent on the canescent bracts of *A. patens* var. *patentissimus*.

One of the more common traits of the section *Patentes* is the presence of biseriate, capitate, glandular trichomes, usually less than 0.25 mm long, especially on the phyllaries. Eglandular plants are found typically only in *A. patens* var. *patentissimus*, while *A. georgianus* and *A. phlogifolius* are often copiously glanduliferous on the upper branches and peduncles.

LEAVES. The basal leaves in *Aster* section *Patentes* are somewhat spathulate, with *A. georgianus* producing the narrowest and *A. phlogifolius* the largest, most serrate basal leaves in the group. The cauline leaves are ovate to lanceolate, with the bases varying from auriculate-amplexicaul in *A. patens* and *A. phlogifolius* to only slightly clasping in *A. georgianus*. In shape and thickness the leaves of *A. georgianus* closely resemble those of *A. grandiflorus* in the related section *Grandiflori*.

The leaves of *A. phlogifolius* average nearly twice as long as those of *A. patens*, but there is so much overlap that this character is not reliable in separating the taxa. Leaf texture and pubescence provide better differences. *Aster phlogifolius* leaves are very thin, wrinkly-rugose, and soft-pubescent,

unlike the unwrinkled, thicker, and scabrous leaves of *A. patens* (Figure 2). These leaf differences persist in transplants, and are evident even in the first few cauline leaves of young seedlings. Leaf textural differences are also useful in distinguishing herbarium specimens of *A. patens* and *A. phlogifolius*, as described in the systematic treatment.

The leaves of *A. georgianus* and *A. patens* are similar in texture and size, although those of the former tend to be more lanceolate, less clasping and thicker, with only a few diffuse veinlets on the lower surface, unlike the fine reticulum of veinlets on *A. patens* leaves. The veinlets are even more diffiuse in the leaves of the dodecaploid *A. grandiflorus*.

The difference in ploidy level between these groups is also evident in epidermal cell size. The larger epidermal cells of *A. georgianus* and *A. grandiflorus* produce a very thick epidermis that will peel away easily in large sheets, while the smaller-celled, and more fragile epidermis of *A. patens* tends to shred when peels are removed. For numerical comparisons, epidermal guard cell pairs were measured in five populations each of diploid *A. patens*, tetraploid *A. patens*, and decaploid *A. georgianus* (R. Jones, 1980, *t. 11*). On the basis of length and width measurements, in microns, of 10 guard cell pairs per leaf, one leaf per plant, and 10 plants per population, the means and ranges were as follows: diploid *A. patens*—22 × 17 (16 × 13 to 29 × 24); tetraploid *A. patens*—27 × 20 (19 × 16 to 36 × 26); and decaploid *A. georgianus*—37 × 30 (24 × 23 to 45 × 39). A similar study of two populations of *A. grandiflorus* revealed that the guard cell pairs of these dodecaploids average, in microns, 44 × 30, and range from 36 × 24 to 55 × 39.

These same size relationships were found to exist in the epidermal guard cells of transplants, seedlings, and even in cotyledons (cotyledon guard cells are much larger than those of cauline leaves). In addition, numerous observations suggest that the number of chloroplasts in these guard cells also varies with the ploidy level, usually 6–8 per cell in diploids, 8–12 in tetraploids, and 12–18 in the decaploids and dodecaploids.

INVOLUCRES. The phyllaries of the *Patentes* occur in from 3–7 series, forming a campanulate to turbinate involucre. The middle phyllaries provide the best taxonomic characters. Variation in the *Patentes* occurs in phyllary size, shape, pubescence, herbaceousness, and in involucral height and shape.

The patterns of involucral variation in *A. patens* are nearly continuous, but there are regional differences in involucral height, phyllary width, and phyllary pubescence, which persist in transplants and seedlings, and thus are assumed to have a genetic basis. Plants in the Interior Highlands tend to have taller involucres with wider, more canescent phyllaries, and are here treated as the var. *patentissimus* (Figures 3, 4). The variety *gracilis* is that group of plants in the southwestern range of the species with shorter involucres and more strigillose phyllaries (Figures 3, 4). Typical *A. patens*

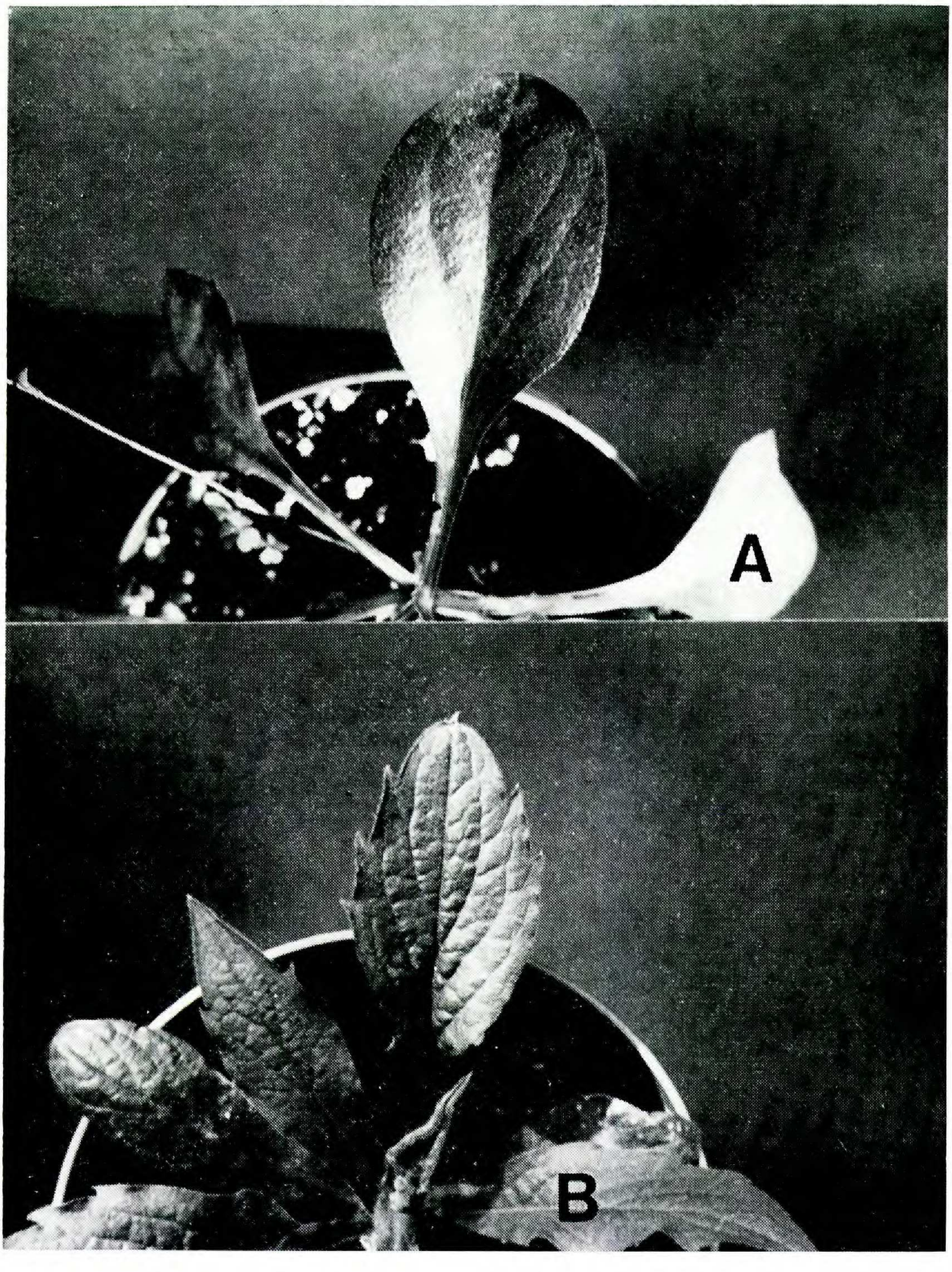

Figure 2. Photographs of seedling basal leaf rosettes of *Aster patens* (A) and *Aster phlogifolius* (B).

of the eastern United States has a campanulate involucre with squarrose, heavily glandular phyllaries (Figures 3, 4).

The involucre also provides species differences in the *Patentes*. In contrast to *A. patens*, the phyllaries of *A. phlogifolius* are loosely imbricated,

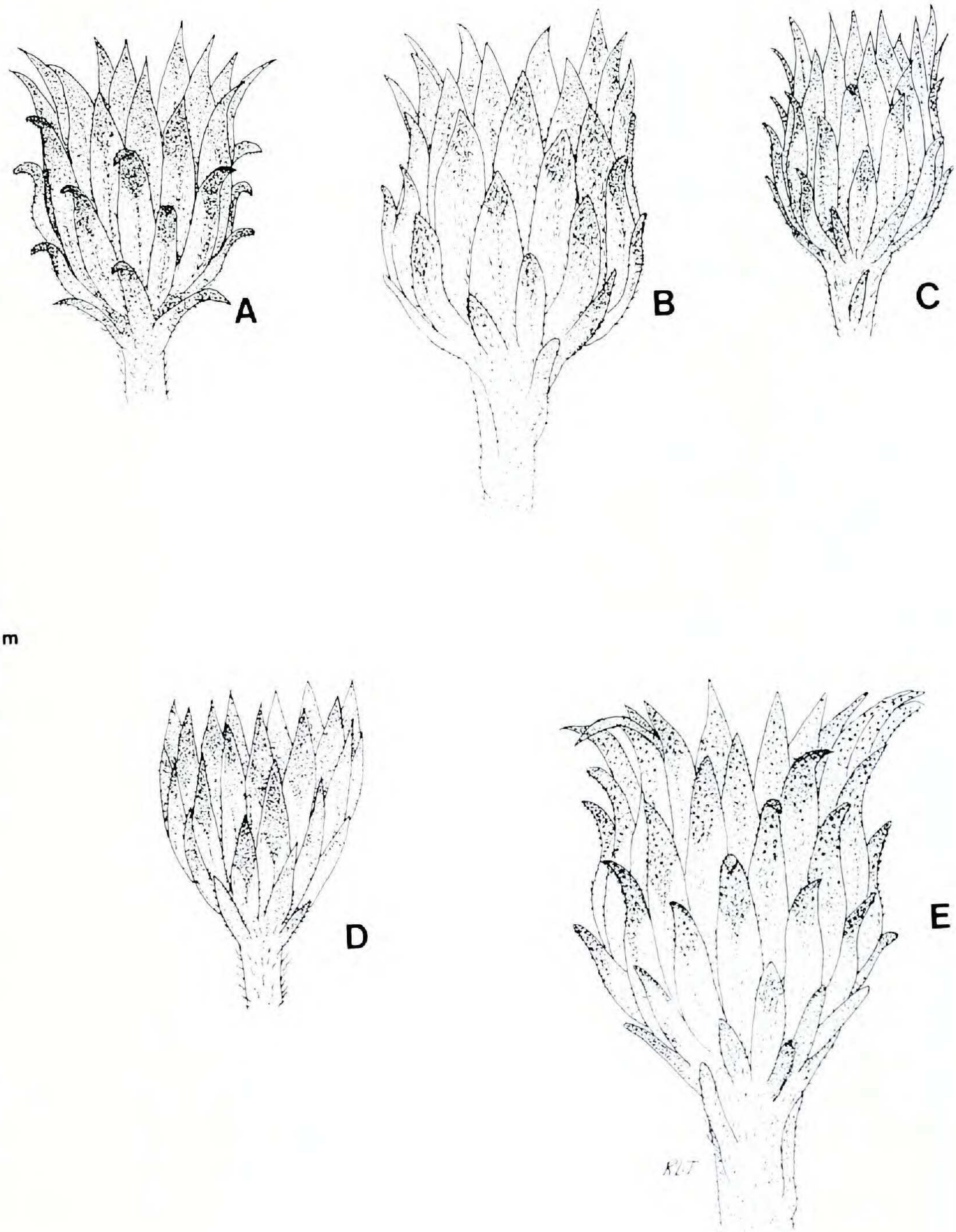

Figure 3. Representative involucres of *Aster patens* var. *patens* (A), *Aster patens* var. *patentissimus* (B), *Aster patens* var. *gracilis* (C), *Aster phlogifolius* (D), and *Aster georgianus* (E).

largely herbaceous, appressed, and glabrate (Figures 3, 5). The involucral differences between *A. patens* and *A. georgianus* are largely those of size. In population studies, the involucral height of diploid *A. patens* averaged 5.7 mm (ranging from 4.5–7.1), that of tetraploid *A. patens* averaged 6.4 mm (ranging from 4.8–8.0), and that of *A. georgianus* averaged 9.0 mm (ranging from 7.8–12.0). As illustrated in Figures 3 and 5, the phyllaries of *A. georgianus* tend to be even more squarrose and more glandular than are those of *A. patens*. The involucre of *A. georgianus* thus approaches that of *A. grandiflorus* in phyllary size and curvature, and these two high-polyploid species are often confused.

FLORETS. As shown in Figures 6 and 7, the disc corollas of *A. phlogifolius* tend to be a little longer, with a more expanded limb and larger lobes, when compared to those of *A. patens*. The largest florets in the group occur in *A. georgianus*, in which the ligules often exceed 2 cm and the disc corolla 1 cm (Figure 8). Total floret number averages fewest in *A. phlogifolius*, with less than 40 florets per head, while the other two species average closer to 50, but there is much overlap.

The best floret difference between the three species is disc corolla color. In *A. patens* the disc corolla is yellow, while in the other two species the disc corolla is white, often with purplish lobes. Evidently these color differences have a genetic basis, for they are maintained in transplants and in plants raised from achenes. In the field, these color differences are very consistent; rarely, *A patens* may produce a whitish disc, but I have yet to find a yellow disc in populations of the other two species. In addition, the yellow disc florets of *A. patens* develop yellow anthers and yellow pollen, while in *A. phlogifolius* and *A. georgianus* the white disc corolla is associated with purplish anthers and whitish pollen. Pollen grain size varies with the ploidy level, averaging about 23 μm in diploid *A. patens*, 25 μm in tetraploid *A. patens*, and 30 μm in decaploid *A. georgianus* (R. Jones, 1980, *t. 14*).

Ligule color in the group varies from nearly white to an intense violet, and can be considerably influenced by the environment. Sporadic pink-liguled plants of *A. patens* occur in the field, but when transplanted produce the normal purplish rays. White-liguled plants occur occasionally in Texas, but the basis of this color difference is yet to be determined.

As measured across the rays, the overall head size in the group varies from about 2.5–3.5 cm in *A. patens* to 5 cm or more in *A. georgianus*. The difference in head size between *A. patens* and *A. georgianus* is usually much more dramatic in greenhouse plants. In cultivation, plants of *A. georgianus* often surpass 1.5 cm in involucral height and 6 cm across the rays, reaching even larger dimensions than *A. grandiflorus*, and possibly the largest head size in the entire genus. Only under very stressful conditions will *A. georgianus* produce heads similar in size to those of *A. patens*.

ACHENES. The achene of *A. patens* is usually gray to brown, with paler

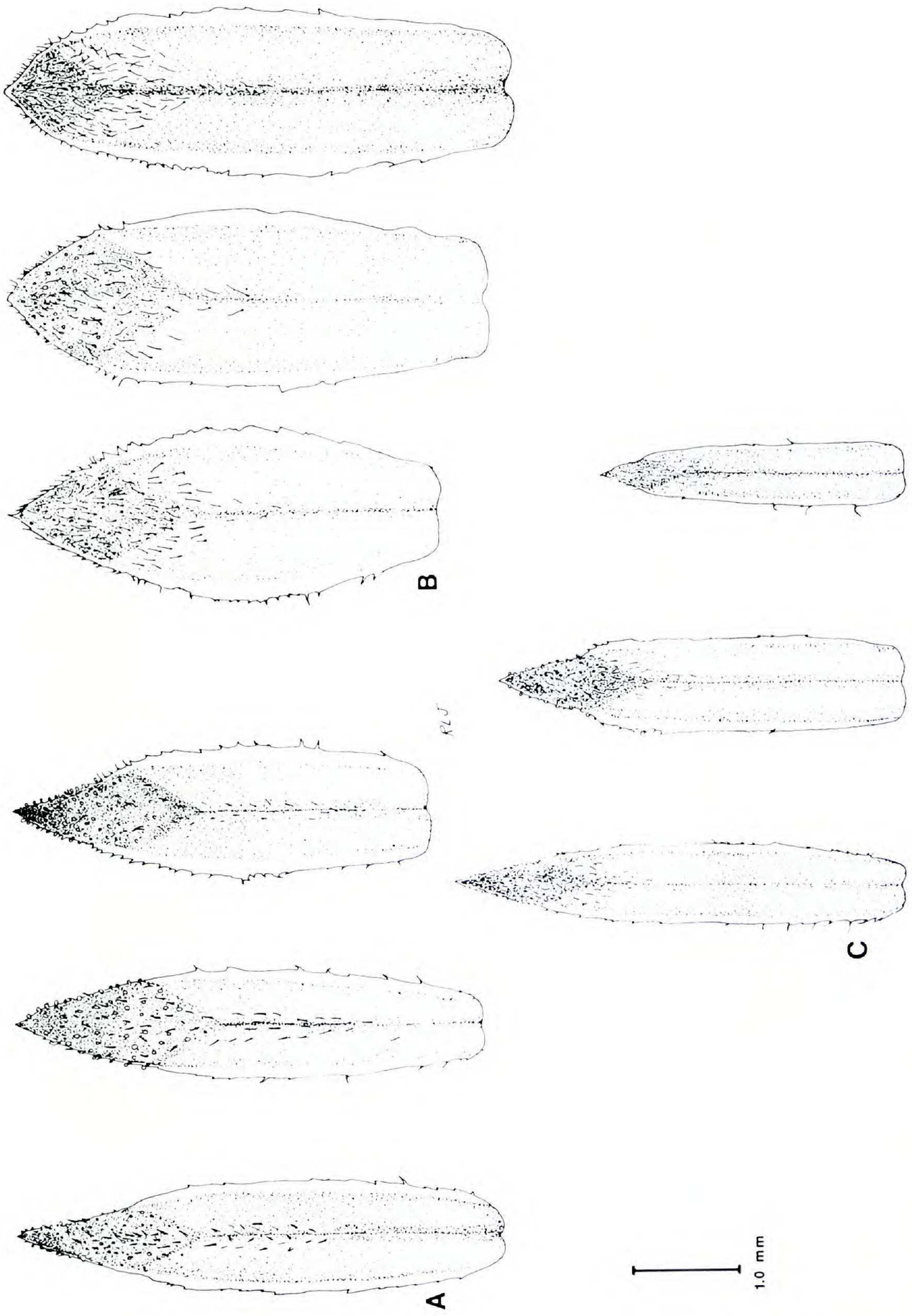

Figure 4. Representative middle phyllaries of *Aster patens* var. *patens* (A), *Aster patens* var. *patentissimus* (B), and *Aster patens* var. *gracilis* (C).

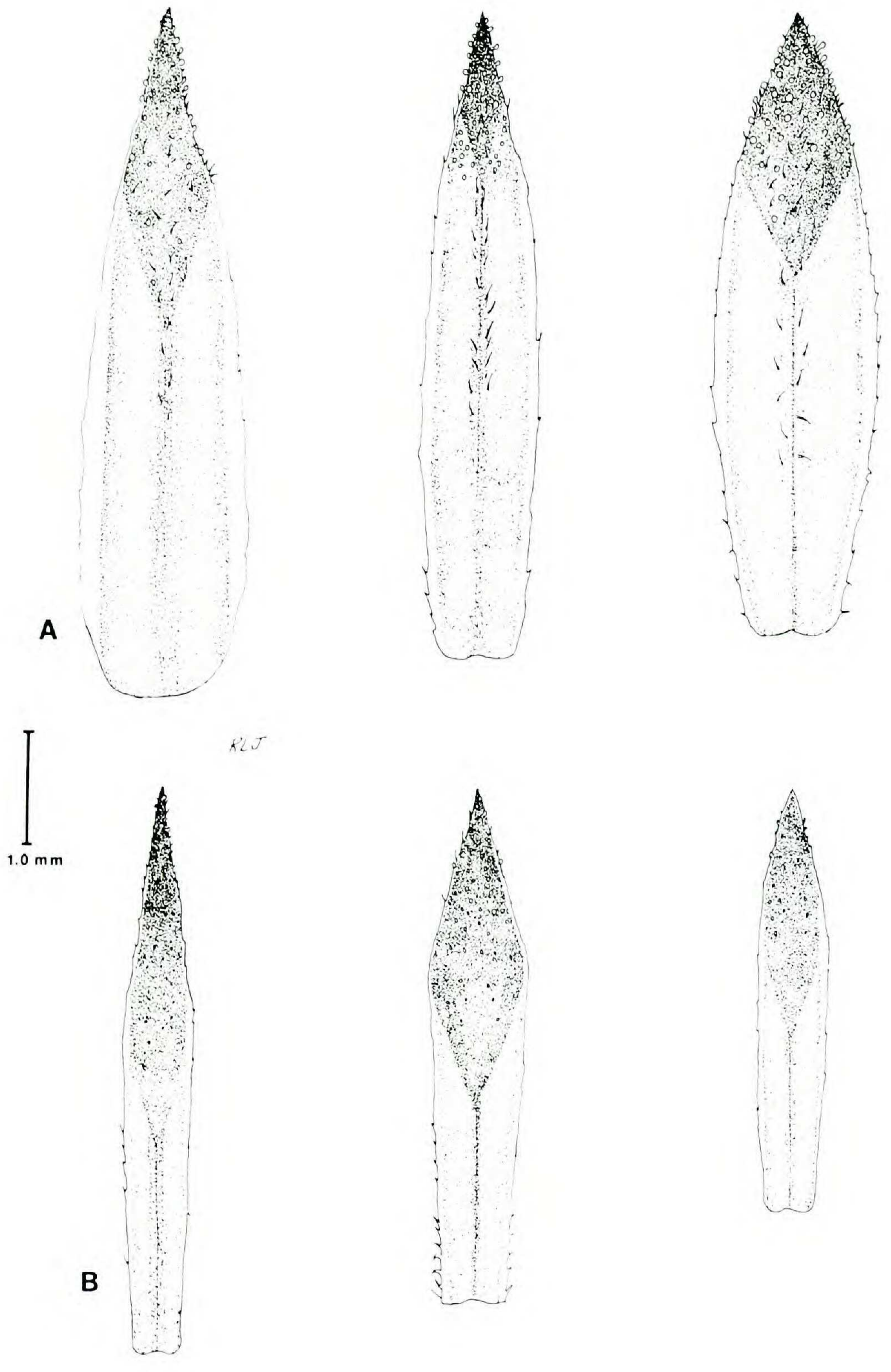

Figure 5. Representative middle phyllaries of *Aster georgianus* (A) and *Aster phlogifolius* (B).

ribs and evenly distributed, somewhat spreading trichomes (Figure 6). The achenes of *A. georgianus* are similar, but more slender and longer (Figure 8). In *A. phlogifolius*, however, the achenes are uniquely different. They are prominently ribbed, bulkier, nearly black, and with the trichomes very short, densely appressed, and restricted to the ribs (Figure 7). The pubescence thus appears to be in whitish lines on the dark achene of *A. phlogifolius*.

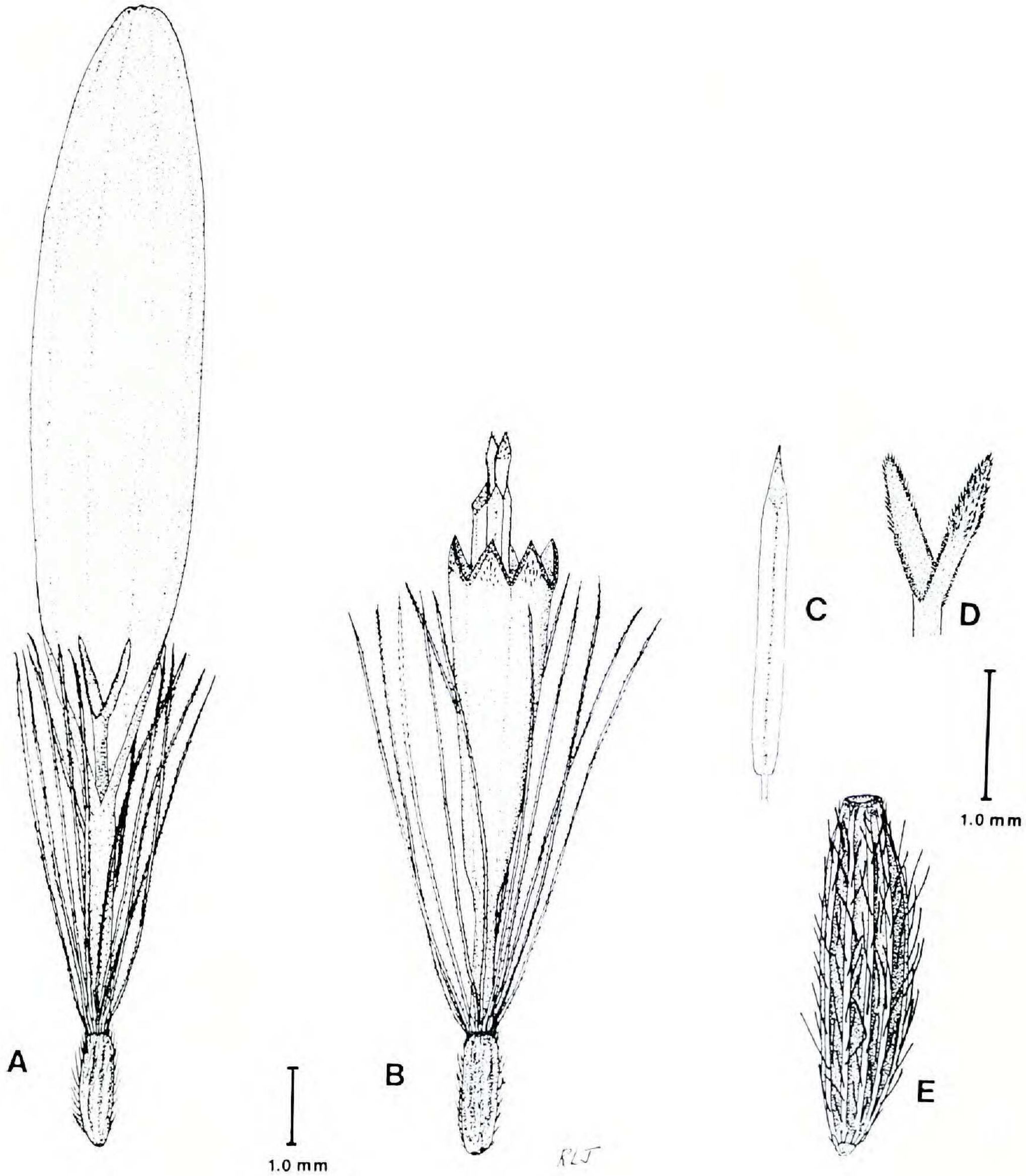

Figure 6. Representative ray floret (A), disc floret (B), anther (C), disc stigmatic branch (D), and achene (E) of *Aster patens*.

CROSSING STUDIES

A tabular presentation of the results of 394 crosses is given in my dissertation (R. Jones, 1980, *t. 17*). To summarize, the crosses within ploidy levels were relatively successful (20–40% average seed set), while crosses between ploidy levels were much less successful (less than 5%), except in the case of the high polyploids.

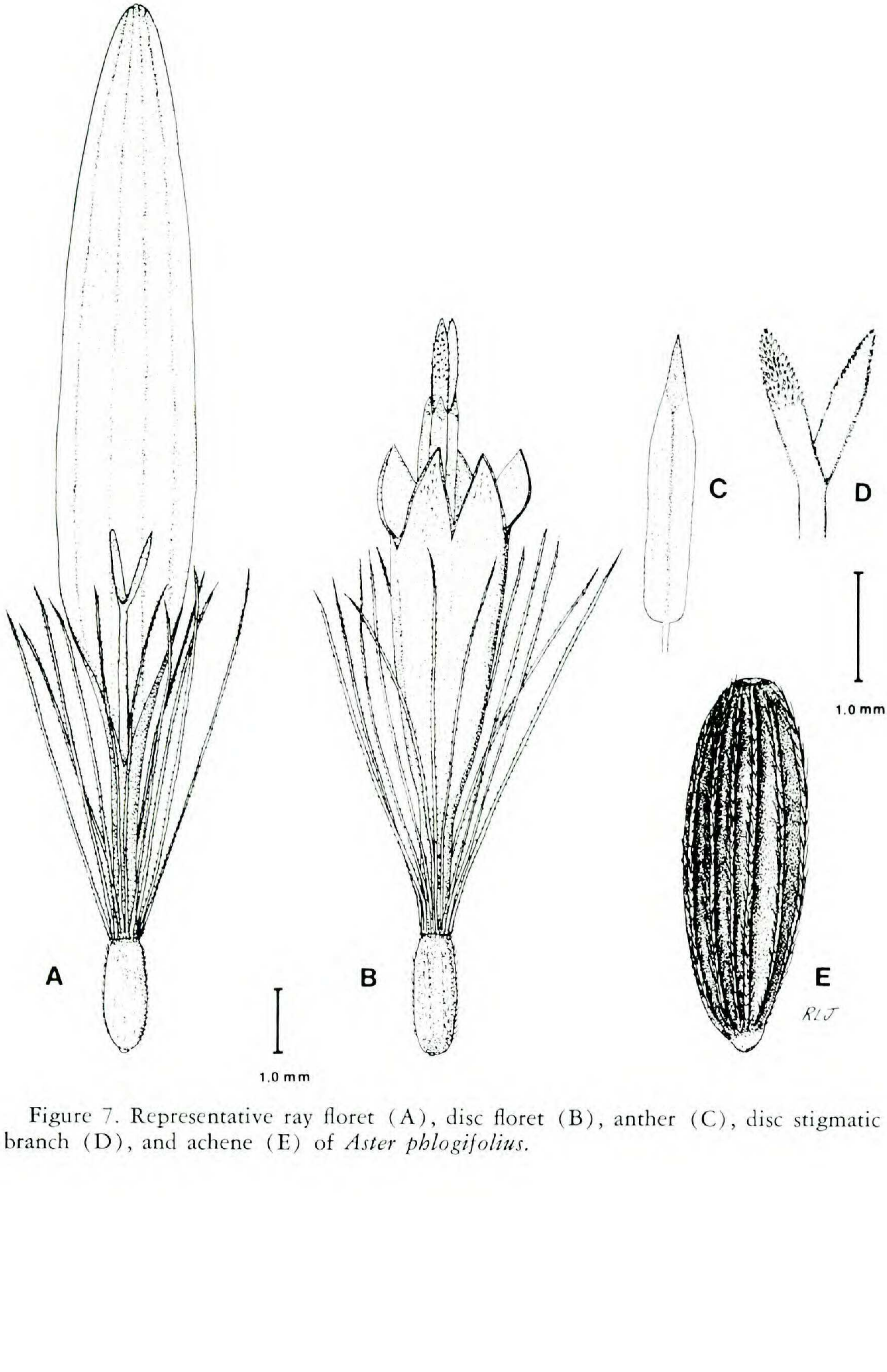

Figure 7. Representative ray floret (A), disc floret (B), anther (C), disc stigmatic branch (D), and achene (E) of *Aster phlogifolius*.

The crossing program demonstrated a good degree of genetic compatibility between tetraploid *A. phlogifolius* and tetraploid *A. patens*—crosses between the taxa were just as successful as crosses within the taxa. Hybrid achenes produced plants with intermediate morphologies. Likewise, the

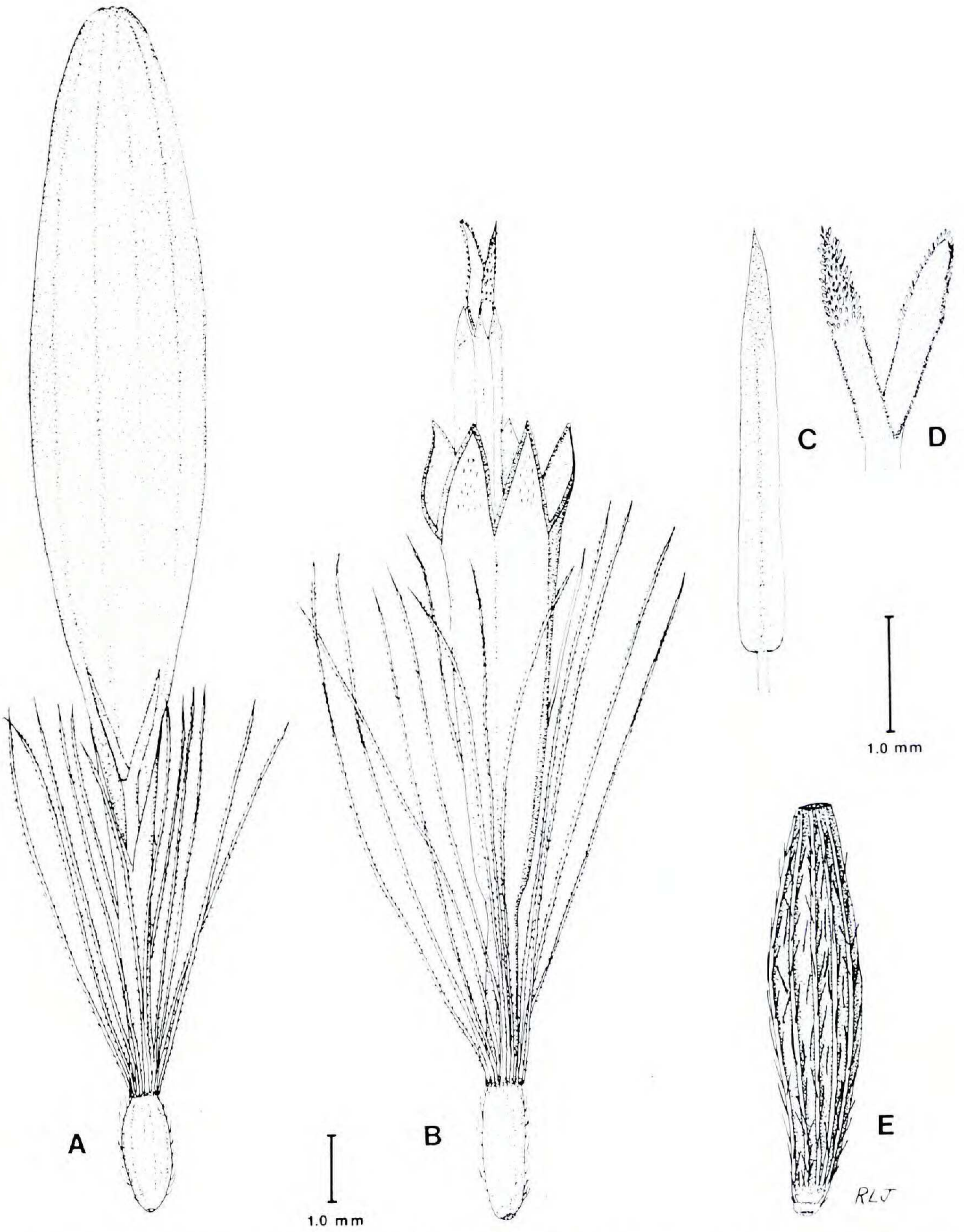

Figure 8. Representative ray floret (A), disc floret (B), anther (C), disc stigmatic branch (D), and achene (E) of *Aster georgianus*.

tetraploid crosses between the varieties *patens* and *patentissimus* of *A. patens* also produced good seed sets, and the hybrid offspring were intermediate in morpology. Only a few crosses were attempted between diploid and tetraploid *A. patens*, and none of these were successful.

Barriers to hybridization were also apparent in the 10 *A. patens* × *A. georgianus* and 15 *A. patens* × *A. grandiflorus* crosses; only a few achenes were produced in these crosses, and none would germinate. One of the more surprising aspects of the crossing studies was the degree of success in hybridizations between *A georgianus* and *A. grandiflorus*, in which 11 crosses produced an average seed set of 20%. Some of these hybrid achenes were germinated, and they persisted for a while as seedlings rosettes, but did not bolt.

ECOLOGY AND DISTRIBUTION

The members of *Aster* section *Patentes* are woodland plants of the eastern United States. Like other perennial asters, they are genetically self-sterile and insect-pollinated, over-wintering as rosettes, bolting in the spring, and flowering in the fall. Peak flowering occurs in late September in *A. phlogifolius*, in early October in *A. patens*, and in late October in *A. georgianus*. Pollination is effected by a number of insects, including bees, butterflies, moths, and beetles. The achenes mature about one month after pollination and seed set is high. Achenes germinate readily in *A. georgianus* and *A. patens* (both upland and lowland populations), but the achenes of *A. phlogifolius* will germinate well only if stratified.

ASTER GEORGIANUS. Of the three species in the *Patentes, A. georgianus* is by far the most limited in distribution, occurring only from eastern North Carolina to central Alabama. These decaploid populations occur very infrequently through this region, and are found primarily in oak-pine woodlands in clay-loams or sandy-clays. At four sites in the St. Clair-Etowah County region of Alabama, I found mixed populations of *A. georgianus* and tetraploid *A. patens*. These plants were often completely intermixed, with individuals of each species growing side by side. In these situations the decaploids are easily distinguished by their colonial habit, much larger heads, deep-violet rays, and white discs. The difference in flowering period is very noticeable in these mixed populations when, in late October, *A. patens* is finishing its flowering period and *A. georgianus* is just coming into full bloom. There was no evidence of natural hybridization between the two ploidy levels in these mixed populations.

The range of *A. georgianus* meets that of *A. grandiflorus* in the Carolinas, and I have found populations of these species within a mile of each other in Montgomery County, North Carolina. The overlap in range and the similarity in habitat would thus offer opportunities for natural hybridizations. A few specimens of *A. georgianus* collected in this region did vary more toward *A. grandiflorus* than does typical *A. georgianus*.

ASTER PHLOGIFOLIUS. Populations of this species occur only in the Appalachians and adjacent regions, and are especially common in the mountainous areas of West Virginia, Virginia, Tennessee, North Carolina, and Kentucky. *Aster phlogifolius* is a plant of cool, mesic, mixed-hardwood communities, mostly at elevations of 300 to 1000 meters. Because of different ecological preferences, *A. phlogifolius* and *A. patens* usually do not occur in mixed populations, although there may be some marginal population contact in the case of habitat disturbance. I located three such sites in the Cumberland Plateau region where both taxa were present. In these situations, in the area of disturbance, individuals of each species can be found growing side by side, with *A. phlogifolius* easily distinguished by its large rugose-veiny leaves, appressed phyllaries, and white disc. There were a few individuals at one site that appeared to be hybrids, but the populations remained distinct, and there was no evidence of introgression. Except for *A. patens*, no other base-5 aster was found in association with *A. phlogifolius.*

ASTER PATENS. There are reports of *A. patens* from every state east of the Mississippi River except Wisconsin, Michigan, Vermont, and Maine. West of the Mississippi River the species occurs in Louisiana, Arkansas, Missouri, Oklahoma, Kansas, and Texas. There is a single record of the species from near Ottawa, Canada, and from an unspecified location in Minnesota (possibly a label error). Herbarium records provide no evidence of *A. patens* in either Mexico or in southern Florida, although it has been reported from the latter region by Ledin (1951).

Populations of this species can be found in almost any upland, acidic, open woodland throughout its range, although less commonly on the outer Coastal Plain, and they occur on a variety of soils. Plants can be found on the dry sands of the Coastal Plain at or near sea level, and in more mesic situations in the Appalachian forests at elevations up to 1000 meters or more. *Aster patens* occurs on the red clays of Georgia, the Black Belt chalks of Alabama, and the prairie-transition soils of Oklahoma. Plants are most common in the full sun or partial shade of woodland borders, but also occur along roadsides, edges of fields, under power lines, and in other recently distured places. There is no obvious difference in habitat among the three varieties of *A. patens.*

The Mississippi Embayment forms a boundary line between var. *patens* in the east and var. *patentissimus* in the Interior Highlands. In these uplands one also encounters populations of typical var. *patens,* as well as populations of intermediate morphologies. Because both varieties are largely tetraploid, these intermediate plants are probably the result of natural hybridization.

Aster patens var. *gracilis* is a largely diploid group of the southwest, from western Alabama to Texas and Oklahoma. Occasional tetraploid populations, some indistinguishable from diploids, others more like the var. *patens* or the var. *patentissimus*, also occur within this range. No evidence was found for

the existence of diploid and tetraploid plants in the same population, although these ploidy levels were found in adjacent counties in western Alabama. Diploid plants are apparently absent from the Atlantic Coastal Plain.

Because diploid counts have been reported from only as far east as Sumter and Baldwin Counties in Alabama, a demarcation line must exist in south central Alabama beyond which diploids do not occur. According to Harper (1943), the western section of the Red Hills of Alabama is more fertile and receives more summer rain than does the eastern section. Garden and greenhouse studies have suggested that the diploids are less hardy than the tetraploids. Thus, perhaps the harsher conditions of the eastern Red Hills somehow have prevented the eastern migration of the less tolerant diploids onto the Atlantic Coastal Plain.

Because of habitat differences there are relatively few opportunities for *A. patens* to hybridize with base-5 asters from other sections. In field studies I have observed the following species of known or presumed base-5 asters in the vicinity of populations of *A. patens*—*A. novae-angliae, A. oblongifolius, A. adnatus, A. concolor,* and *A. pratensis.* Others to be expected include *A. grandiflorus, A. walteri* and *A. sericeus.* Only in the instance of contact with *A. oblongifolius* was there evidence of hybridization—a single individual in a population of *A. patens* var. *patentissimus* in Fulton County, Arkansas, varied toward *A. oblongifolius* in leaf and involucre. Hybrids between these two species have also been reported by Correll and Johnston (1970). Plants that Radford et al. (1968) described as intermediate between *A. patens* and *A. grandiflorus* are probably collections of *A. georgianus.* Other base-5 asters of the U. S. are inhabitants of grasslands, prairies, and coastal marshes, and thus would be less likely to come into contact with populations of *A. patens.*

SPECIES CONCEPT

The concepts of species and varieties followed in this study fall within the limits of the definitions proposed by Cronquist (1978). I have chosen to instate *A. georgianus* and *A. phlogifolius* to species rank because of the existence in these taxa of consistent morphological variation patterns involving readily observable features of the entire plant body (from rhizome to involucre to achene), which has a genetic basis (features retained in transplants, seedlings, and in mixed populations with *A. patens*), which are explainable by isolating mechanisms (ecological in *A. phlogifolius* and chromosomal in *A. georgianus*), and which are discontinuous with those of *A. patens.* Two other taxa, the var. *gracilis* and var. *patentissimus* of *A. patens*, are retained at the varietal level because the features are less consistent, are mostly restricted to the involucre, and show more continuity with the typical features of *A. patens* var. *patens,* but are based on genetic differences which have geographic correlations.

Crossing studies indicate that tetraploid *A. phlogifolius* and tetraploid *A. patens* will hybridize, but that diploid *A. patens* is incompatible with tetraploid *A. patens*. The section *Patentes* thus provides an excellent example of the taxonomic conflict encountered in *Aster* when morphological divergence has not been accompanied by reproductive divergence, and vise versa. In addition, *A. patens* and *A. georgianus* provide examples of groups in which both morphological and reproductive divergence have taken place. If priority were given to incompatibility relationships, then *A. phlogifolius* could not be recognized as a species, and the diploid plants in *A. patens* would have to be segregated as a distinct species. In neither instance would the resulting taxonomy reflect the comparative morphological differences that are actually observable in nature.

PHYLOGENY

The best clues to the evolutionary history of the *Patentes* are found in the cyto-geographic relationships. The distribution of the diploids (*A. patens* var. *gracilis*), which are presumably ancestral to the other taxa, suggests a southwestern, or possibly even a Central American origin of the group. A significant development in the evolution of the group was the appearance of tetraploid plants, which, with their greater ecological tolerance, could expand the range of the group to the east and the north. Geographic isolation of tetraploids in the Interior Highlands by the Mississippi Embayment would then account for the morphological divergence of *A. patens* var. *patentissimus*. *Aster phlogifolius* is apparently the result of ecological isolation of tetraploid populations in the mesic habitats of the Appalachians.

The origin of populations of *A. georgianus* with the perplexing chromosome number of $2n=50$ is at this point still unclear. The large gap in chromosome numbers between this group and the known ploidy levels in *A. patens* suggests that these colonial decaploids are not simple polyploid derivatives of diploids and tetraploids. Another fact to be considered is that, although *A. georgianus* is morphologically very similar to *A. patens*, there are also some resemblances to *A. grandiflorus*, especially in leaf and involucre. One hypothesis, then, is that some kind of crossing event between dodecaploid *A. grandiflorus* and tetraploid *A. patens* was involved in the ancestry of decaploid *A. georgianus*. A $2n$ number of 50 could be obtained from plants with $2n=60$ and $2n=20$ in several ways. For example, if a somatically reduced pollen grain of *A. grandiflorus* (15 chromosomes) fertilized a reduced egg of *A. patens* (10 chromosomes), then the offspring would have 25 chromosomes, which could then double to 50. With its intermediacies in leaf, involucre, and head size, a mature offspring of *A. patens* and *A. grandiflorus* would, in theory, look very much like *A. georgianus*.

Whatever their origin, these decaploids now behave as a species, with a distinct geographic range, chromosome number, and morphology. The evidence for the implication of *A. grandiflorus* is purely circumstantial, and

there are, of course, other possible explanations for the origin of these decaploid populations. In the absence of experimental verification, the ancestry of *A. georgianus* remains a mystery.

SYSTEMATIC TREATMENT

ASTER section PATENTES T. & G., Fl. N. Amer. 2: 114. 1841.

Lasallea Greene subsect. *Brachyphyllae* (T. & G.) Semple & Brouillet, Amer. J. Bot. 67: 1023. 1980. In part.

Virgulus Raf. section *Patentes* (T. & G.) Reveal & Keener, Taxon 30: 650. 1981.

Perennial herbs from a thickened caudex or a creeping rhizome. Stems, branches, and leaves pubescent with appressed to spreading, uniseriate, tapering trichomes, often glandular with biseriate, capitate trichomes. Rosette and lower stem leaves soon deciduous, obovate-spathulate to oblanceolate-spathulate, 5–12 cm long and 1–5 cm wide, acuminate to obtuse, mucronulate, entire-ciliate, or with a few scattered teeth, variously attenuated to a sheathing or clasping base, the surfaces strigose to pilose. Cauline leaves less than 30 below the inflorescence, ovate to ovate-oblong to lanceolate, 2–15 cm long and 1–4 cm wide, varying with the species, acuminate to obtuse, mucronulate, entire-ciliate or with a few teeth, sessile and cordate-clasping to auriculate-amplexicaul, texture and venation variable, surfaces soft-pubescent to scabrous. Inflorescences paniculiform to racemiform; peduncular bracts mostly 2–4 mm, much smaller than upper cauline leaves. Involucre campanulate to turbinate, 5–12 mm tall, the phyllaries imbricated in 3–7 series, gradually shortened from innermost to outermost, middle phyllaries linear-lanceolate to somewhat oblanceolate, acuminate to obtuse, entire to hyaline-fimbriolate; upper portion of the phyllary herbaceous and squarrose or appressed, tha basal portion chartaceous-indurate, puberulent toward the apex and down the midvein with glandular and non-glandular trichomes, in varying amounts. Heads radiate, mostly 2–3 cm across the rays, up to 5 cm in one species, with 30–70 florets per head. Ray florets with pappus about 1/3 as long as the ligule; ligules lavender to deep-violet, sometimes pink or white. Disc florets with pappus nearly as long as the disc corolla; disc corolla yellow or white, depending on the species, the lobes often purplish, the whole corolla becoming so with age, the corolla differentiated into a narrow tube and broader limb with 5 triangular erect to spreading lobes. Stamens yellow or purplish, pollen yellow or white, both features varying with the species. Achenes light gray-brown to nearly black, 2–4 mm long, the longitudinal ribs often 10 or more, surfaces pubescent, the trichomes made up of two elongate, parallel cells, these restricted to the ribs in one species. $2n = 10$, 20, 50, with occasional B-chromosomes in the diploids and tetraploids.

Distribution: Woodland borders and open places of the eastern United States.

TYPE SPECIES: *Aster patens* Ait. Hort. Kew. 3: 201. 1789.

KEY TO THE TAXA OF ASTER SECTION PATENTES

1. Plants colonial, the stems arising singly from elongate rhizomes. Leaves thick and scabrous, the veinlets diffuse on lower surface, or with areoles over 1 mm across, tht leaf base only slightly clasping. Branches thick and strongly ascending. Involucre 8–12 mm tall, phyllaries both squarrose and glandular-strigillose. Disc florets 8–10 mm tall, white with purplish lobes, anthers purplish and pollen white. Heads over 4 cm across the rays.....1. *Aster georgianus*
1. Plants cespitose or with single stems arising from caudices, rarely with elongate rhizomes. Leaves various but with distinct reticulum on lower surfaces, the areoles less than 1 mm wide. Branches slender and spreading to ascending. Involucres and florets without the above set of features. Heads less than 4 cm across the rays.
2. Cauline leaves large and thin, usually over 80 mm long, the upper surfaces rugose-veiny and wrinkled, when dried and magnified appearing smooth and dull, dark green, both surfaces softly pubescent. Involucres short-cylindric, phyllaries loosely imbricated in 3–4 series, appressed, over 50% green, glandular but not strigillose. Disc corollas and pollen white, anthers purplish. Achenes large, often over 3.5 mm long, dark brown to black, the trichomes less than 0.4 mm and restricted to the ribs, the pubescence thus appearing to be in lines .....2. *Aster phlogifolius*
2. Cauline leaves usually less than 80 mm long, the leaves thick, venation inconspicuous, the surfaces appearing ridged and glistening when dried and magnified, scabrous. Involucre campanulate to turbinate, phyllaries in 4–7 series, either squarrose and strigillose or appressed and canescent, largely indurate. Disc corollas, anthers, and pollen yellow. Achene slender, gray to brown, the trichomes long and ascending, occurring both on and between the ribs. .....3. *Aster patens*
3. Involucres turbinate, usually over 8 mm tall, the phyllaries often in 5–7 series, over 1.2 mm wide, obtuse, appressed, sparsely glandular to eglandular, densely strigillose to canescent .....3c. *Aster patens* var. *patentissimus*
3. Involucres campanulate, less than 8 mm tall, phyllaries in 4–5 series, less than 1.2 mm wide, acute to acuminate, sparsely to densely glandular, sparsely to densely strigillose.
4. Plants slender, long-branches, with involucres less than 6.5 mm tall, the phyllaries sparsely glandular and densely strigillose.....3b. *Aster patens* var. *gracilis*
4. Plants more robust, involucres often over 6.5 mm tall, the phyllaries densely glandular and sparsely strigillose.....3a. *Aster patens* var. *patens*

1. ASTER GEORGIANUS Alexander in Small, Man. Fl. SE. U.S., 1381. 1933.

Aster patens Ait. var. *georgianus* (Alexander) Cronquist, Brittonia 29: 218. 1977.
Virgulus patens (Ait.) Reveal and Keener var. *georgianus* (Alexander ex Small) Reveal and Keener, Taxon 30: 650. 1981.

Plants colonial, with new stems arising singly at some distance from the old stem bases. Underground stems elongate and creeping, the rhizomes usually lacking a caudiciform portion. Stems, branches, and leaves scabrous with stiff, swollen-based, ascending trichomes, often copiously glanduliferous. Stems erect, branches few, thick and strongly ascending. Cauline leaves lanceolate to oblanceolate, 30–70 mm long and 10–20 mm wide, the bases narrowed and only slightly cordate-clasping; leaves very thick, upper surface in fresh material with inconspicuous lateral venation, appearing ridged and

glistening when dried and magnified, veinlets diffuse on lower surface, the reticulum indistinct or the ultimate areoles less than 1 mm in diameter, the epidermal layer thick and peelable in large sheets. Inflorescences narrowly racemiform or paniculiform, with one or a few heads at ends of ascending branchlets; peduncles sometimes over 10 cm long, the peduncular bracts squarrose to spreading. Involucres turbinate, 8–10(–12) mm tall, the phyllaries 30–50, tightly imbricated in 4–7 series, strongly squarrose, middle phyllaries broadly lanceolate-linear, 5–7 mm long and 1.0–1.7(–2.0) mm wide, acuminate to acute, ciliate to fimbriolate, less than 50% green, both glandular and strigillose. Heads 4–5(–6) cm across the rays, with usually 12–24 ray florets and 20–40 disc florets. Ligules lavender-violet to haematoxylin-violet, 14–24 mm long; disc corollas white with purplish lobes, 7–10(–11) mm long; anthers purplish, mostly 3–4 mm long, the pollen whitish; styles often conspicuously exerted, the appendaged stigmatic branches 1.5–2.5 mm long. Achenes pale gray-brown, slender, 2.5–4.0 mm long, trichomes over 0.4 mm long, scattered both on and between the ribs. $2n = 50$. Figure 9.

Distribution (Figure 10). Oak-pine flatwoods and uplands, especially Piedmont, from North and South Carolina into Georgia and Alabama. Early October to middle November.

TYPE: GEORGIA. Richmond Co.: Augusta, 10 Oct 1898, *Cuthbert* (HOLOTYPE: NY!).

Cronquist (1977), in proposing varietal status, noted that both these large-headed plants and typical *A. patens* occur in similar habitats and that "The nature of the population structure and breeding-behavior that permits this group to retain its identity under such conditions remains to be determined." The present study clarifies both the morphological basis for the recognition of the taxon as a distinct species and the nature of the breeding system that maintains these differences.

Because of head size and leaf shape, *A. georgianus* has sometimes been mistaken for *A. grandiflorus*, or for a hybrid between this dodecaploid species and *A. patens*. In contrast to *A. georgianus*, however, *A. grandiflorus* has a more cespitose habit, with narrower, less clasping leaves, hispid pubescence, abruptly spathulate and foliaceous phyllaries, and yellow disc flowers. Because of range overlap, as well as similarity in chromosome number, there is a possibility that some natural hybridization could take place between these two high-polyploid base-5 asters in the Carolinas.

Herbarium records provide evidence of *A. georgianus* in only 21 counties in the southeastern United States; collections during this study have added four additional counties. All of these records are from the four contiguous Piedmont states, with the exception of a single collection from northern Florida, and a dubious, mixed collection from Louisiana. Despite extensive searches, I was able to find this species at only nine sites, four in Alabama,

one in Georgia, one in South Carolina, and three in North Carolina. *Aster georgianus* is thus an uncommon plant throughout its limited range, and is perhaps deserving of consideration as a threatened or endangered species.

Figure 9. Holotype of *Aster georgianus* Alexander in Small.

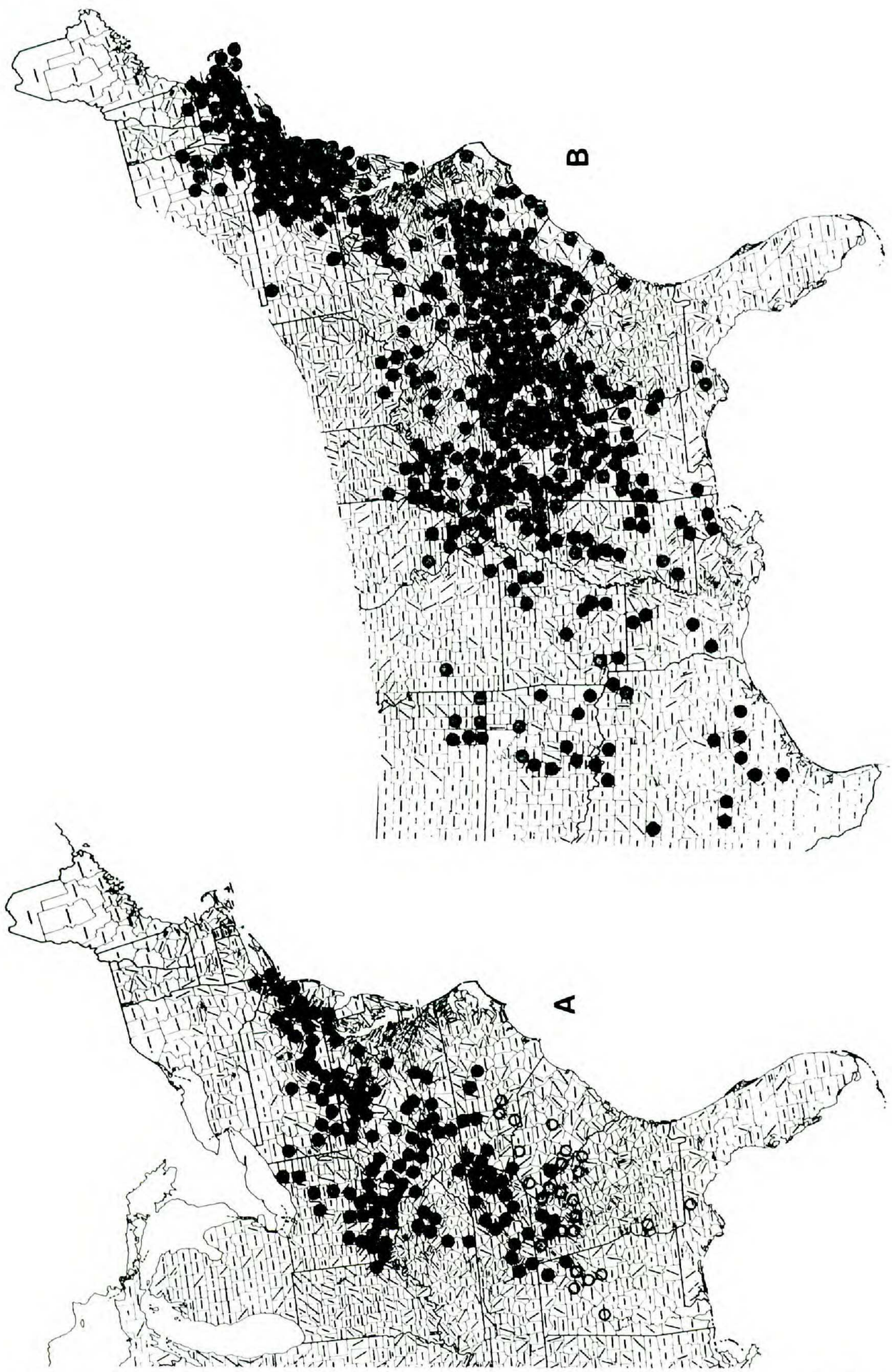

Figure 10. Map A. Distribution of *Aster georgianus* (open circles) and *Aster phlogifolius* (solid circles). Map B. Distribution of *Aster patens* var. *patens*.

2. ASTER PHLOGIFOLIUS Muhl. ex Willd., Sp. Pl., ed. 4, 3: 2034. 1803.

Aster patens Ait. var. *phlogifolius* (Willd.) Nees, Gen. Sp. Aster., 49. 1832.
Aster auritus Lindl. in DC., Prod. 5: 232. 1836. TYPE: An English cultivar of unknown origin, *Lindley* (ISOTYPE: CGE!).
Virgulus patens (Ait.) Reveal & Keener var. *phlogifolius* (Muhl. ex Willd.) Reveal & Keener, Taxon 30: 650. 1981.

Plants solitary-stemmed, or occasionally cespitose, the new stems arising at or near the old stem bases. Underground stem a caudex, short and thickened, not rhizomatous. Stems, branches, and leaves soft-pubescent with slender-based, ascending to spreading trichomes, often copiously glanduliferous. Stems tall and arching, branches few and short, occurring mostly toward the summit. Cauline leaves ovate-lanceolate to panduriform, 75–125 (–140) mm long and 15–35(–40) mm wide, acute to acuminate, strongly cordate-clasping to auriculate-amplexicaul; leaves very thin, almost membranous, upper surface in fresh material rugose-veiny and wrinkled, appearing smooth and dull, dark green between the veinlets when dried and magnified, the veinlets finely reticulate on the lower surface. Inflorescences narrowly racemiform, the heads short-peduncled and often crowded along the arching branchlets; peduncles less than 4 cm long, peduncular bracts appressed. Involucres short-cylindric, 5.5–7.5(–8.0) mm tall, the phyllaries 20–35, loosely imbricated in 3–4 series, appressed, middle phyllaries narrowly linear, 3.5–5.5 mm long, 0.7–1.1 mm wide, acute to acuminate, mostly entire, over 50% green, glandular but not strigillose. Heads less than 4.0 cm across the rays, with usually 9–17 ray florets and 15–35 disc florets. Ligules lavender-violet to haematoxylin-violet, 10–18(–20) mm long; disc corollas white with purplish lobes, 6–8 mm long; anthers purplish, 2–3 mm long, the pollen whitish; styles often conspicuously exerted, the appendaged stigmatic branches 1.5–2.0 mm long. Achenes dark brown to black, bulky, 2.5–4.0 mm long, trichomes less than 0.4 mm long, and appressed, occurring mostly on the ribs, and the pubescence thus appearing in lines. $2n=20$. Figure 11.

Distribution (Figure 10). Rich, mesic, mixed-hardwood forests of the Appalachians, from southeastern New York to northeastern Alabama. Late August to middle October.

TYPE: PENNSYLVANIA. *Muhlenberg* (HOLOTYPE: B, photograph!; possible ISOTYPE: PH!).

Torrey and Gray, in 1841, followed Nees in treating this plant as a variety, but remarked that they were "strongly disposed to consider it a distinct species; but are now convinced by the examination of numerous intermediate forms, that it is a state which the plant assumes in shady moist places." Most later authors have accepted this concept, viewing Appalachian taxon as a shade form or sylvan race of *A. patens*, and deserving of no more than varietal status. This "shade morphology," however, can now be shown to be based on genetic differences, and to be reliable enough for

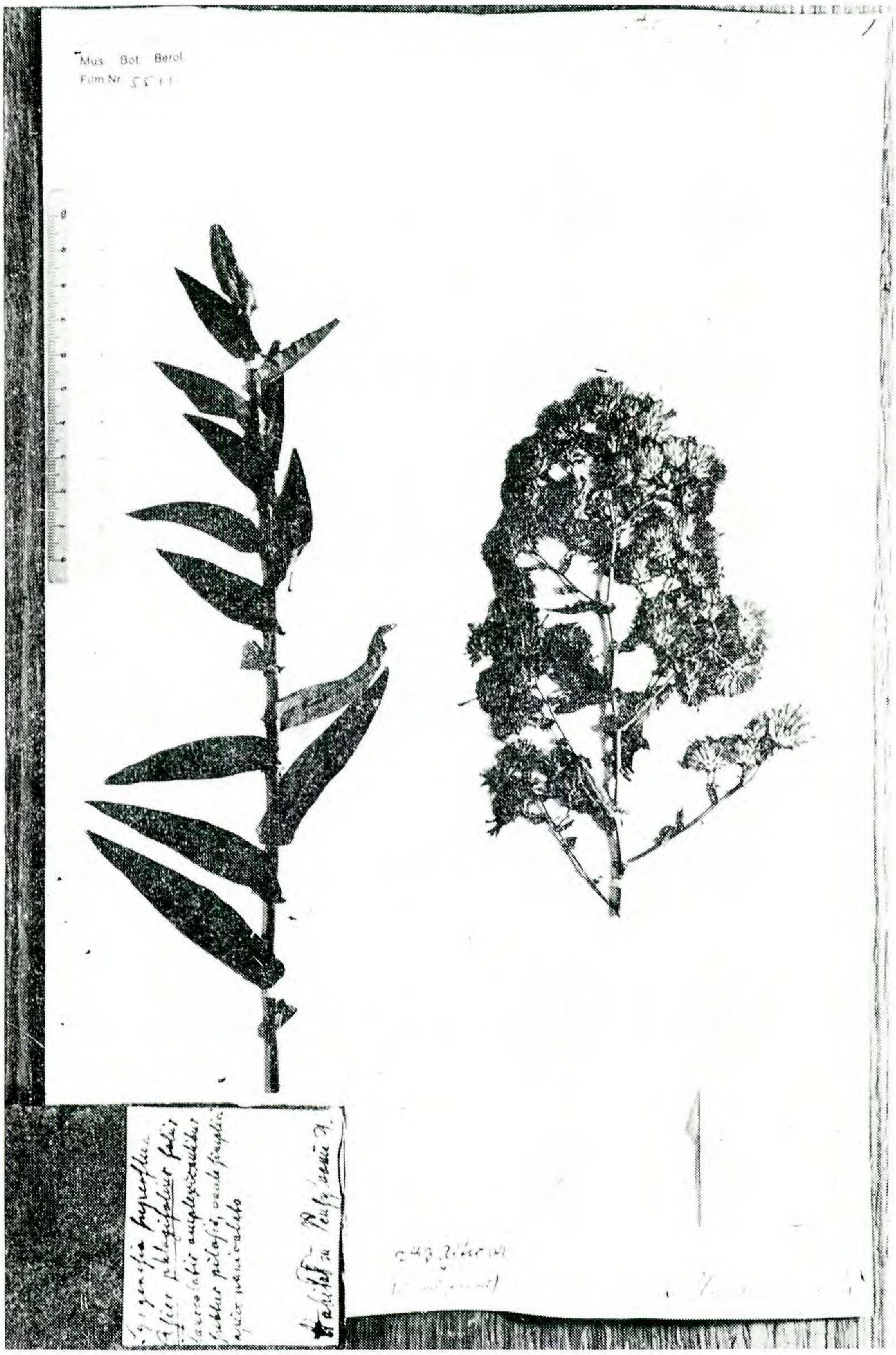

Figure 11. Holotype of *Aster phlogifolius* Muhl. ex Willd. Photograph courtesy of Botanischer Garten und Botanisches Museum, Berlin.

consistent identification of *A. phlogifolius*.

Mesic forms of *A. patens*, with their larger leaves and more racemiform inflorescence, are often misidentified as *A. phlogifolius*. The key differences between these taxa, however, involve leaf texture and pubescence, phyllary texture and pubescence, disc color, and achene pubescence, and the more mesic forms of *A. patens* remain distinguishable from *A. phlogifolius* on the basis of these characters.

Aster patens and *A. phlogifolius* in the Appalachians are tetraploid, and some natural hybridization can be expected in the event of population contact; these opportunities for hybridizations usually occur as a result of habitat disturbance. In most cases, populations of these two taxa are ecologically isolated, and even if there is contact, it is usually only marginal, and the populations remain clearly discernable.

Aster phlogifolius frequently occurs on rich, rocky, loamy, slopes, often above small streams, along and within the forest edge, in full or partial shade. In these situations, the plants are very attractive, with tall, arching, leafy stems, and apical clusters of crowded, deep-violet heads. It is an inhabitant of mature forest lands, and reacts poorly to disturbance; if the canopy is removed and the plants exposed to full sunlight, most will die.

3a. ASTER PATENS Ait. var. PATENS Hort. Kew. 3: 201. 1789.

Aster amplexicaulis Michaux, Fl. Bor.-Amer. 2: 114. 1803, *non* Lamarck (1783), *nec* Muhl. ex Willd. (1803). TYPE: AMERICA. Carolina. *Michaux* (ISOTYPES (3): P!).

Aster patens Ait. f. *rosea Svenson*, Rhodora 37: 263. 1935. TYPE: "New York, Oct 11, 1931," *Svenson 4727*, in Brooklyn Botanic Garden Specimen not seen.

Lasallea patens (Ait. Semple & Brouillet, Amer. J. Bot. 67: 1023. 1980.

Virgulus patens (Ait.) Reveal & Keener, Taxon 30: 650. 1981.

Plants cespitose, with new stems arising in clusters at or near the old stem bases. Underground stem a caudex, or occasionally with short rhizomes. Stems, branches, and leaves scabrous with stiff, swollen-based, ascending trichomes. Stems ascending to erect, branches many, slender, and divaricately spreading. Cauline leaves ovate to oblanceolate, (20-)30–70(-90) mm long and 10–30(-40) mm wide, acuminate to obtuse, the base broadened and cordate-clasping to auriculate-amplexicaul; leaves thick, upper surface in fresh material with inconspicuous lateral venation, appearing ridged and glistening when dried and magnified, the veinlets on the lower surface forming a distinct reticulum with ultimate areoles often less than 0.5 mm across. Inflorescences usually paniculiform, with one or a few heads at ends of spreading branchlets; peduncles short to elongate, often over 10 cm long, the peduncular bracts appressed to squarrose. Involucres campanulate, 5.5–7.5 (-8.5) mm tall, the phyllaries 25–45, tightly imbricated in 4–6 series, squarrose, middle phyllaries linear to lanceolate, 3.5–5.5 mm long and 0.8–1.2(-1.5) mm wide, acuminate to acute, ciliate to fimbriolate, less than

50% green, strigillose, but prevailingly glandular, the capitate trichomes large and conspicuous at 30×. Heads less than 4 cm across the rays, and usually 12–24 ray florets and 20–50 disc florets. Ligules pale lavender to pleroma violet or mauve, sometimes white or pink, 10–18(-20) mm long; disc corollas yellow, paler toward the base, rarely whitish, 5.5–7.5 mm long; anthers yellow, 2–3 mm long, the pollen yellow; styles only slightly surpassing the corolla, the appendaged stigmatic branches 1.0–1.5 mm long. Achenes tan to dark-brown or grayish, slender, 2.0–3.5 mm long, the trichomes scattered both on and between the ribs, usually over 0.4 mm long and spreading. $2n=20$, 10. Figure 12.

Distribution (Figure 10). Dry woodland borders and open places, especially oak-pine and oak-hickory, throughout much of the eastern United States, less frequent on the outer Coastal Plain and in the ranges of the other two varieties. Late August to early November.

TYPE: A cultivated specimen from the Chelsea Physic Garden, *Miller* (HOLOTYPE: BM, photograph, NY!).

The variety *patens* is representative of the species as it was originally described. Because of its taxonomic distinctiveness, *A. patens* has long been recognized as a clearly definable species of the eastern United States, although there was some early confusion with *A. undulatus* L., a base-8 species with cordate-petiolate basal leaves and clasping cauline leaves, and there are still many misidentifications involving these two species. The majority of populations making up the var. *patens* are tetraploid and occur east of the Mississippi River. These tetraploids are a versatile group, being capable of reacting favorably to disturbance, and occurring in more kinds of habitats than either *A. phlogifolius* or *A. georgianus*. With their hardiness, long flowering period, and cold-independent achenes, these plants illustrate a generalized adaptation which enables populations of *A. patens* to survive and reproduce under a variety of climatic and edaphic conditions.

3b. ASTER PATENS Ait. var. GRACILIS Hooker, Companion Bot. Mag. 1: 97. 1835.

Aster patens Ait. (var.) *tenuicaulis* C. Mohr, Pl. Life Alabama, 780. 1901. TYPE: Same type as in *A. patens* Ait. var. *gracilis* Hook.

Aster tenuicaulis (Mohr) Burgess in Small, Fl. SE. U. S., 1903.

Virgulus patens (Ait.) Reveal & Keener var. *gracilis* (Hook.) Reveal & Kenner, Taxon 30: 650. 1981.

Plants differing from the typical variety in the less glandular pubescence, the generally more slender nature of the stems and branches, the cauline leaves usually less than 5 cm long and 2 cm wide, but the differences especially evident in the involucral and floral features. Involucres 4.5–6.5 mm tall, the middle phyllaries 3–4 mm long and 0.7–1.0 mm wide, indument predominantly strigillose, the glandular trichomes usually present but few

Figure 12. Photograph of holotype of *Aster patens* Ait.

and inconspicuous at 30×. Heads usually less than 3 cm across the rays. Ray florets with ligules 8–12 mm long. Disc. florets with corollas 4.5–6.5 mm long, the anthers 2.0–2.5 mm long. Mature achenes 2.0–3.0 mm long. $2n=10$, 20, 1–2 B-chromosomes in the diploids. Figure 13.

Distribution (Figure 14). Dry oak-pine and oak-hickory woodlands from western Alabama (Black Belt and western Red Hills) to Texas and Kansas. Late August into November.

TYPE: LOUISIANA. Washington Parish: Jacksonville, 1833, *Drummond* (LECTOTYPE: here designated K!; ISOLECTOTYPES: GH!, K!, PH!).

Noting that "Mr. Nuttall considers them distinct," Hooker (1835) coined the varietal epithet *gracilis* to describe the slender, long-branched, and small-leaved specimens of *A. patens* collected by Drummond near Jacksonville, Louisiana. Although this varietal name has been used by some authors to refer to slender, long-branched plants in both the Gulf and Atlantic Coastal Plains, the variety *gracilis* is here viewed in the sense of Torrey and Gray (1841) as a southwestern taxon, reaching its eastern limit in western Alabama. This position is taken because there is a demonstrable correlation between the southwestern distribution, involucral and floral dimensions, involucral pubescence, and the diploid condition.

The morphological differences between diploids and tetraploids in *A. patens* are primarily quantitative; the best macroscopic indicators of diploidy are slender stems, short involucres, narrow and prevailingly strigillose phyllaries, and smaller florets. Diploids also average smaller in guard cells (22 × 17 μm) and in pollen grains (23 μm) than do tetraploids (27 × 20 for guard cells and 25 μm for pollen). There are, however, no sharp breaks in the variation patterns of any of these features that would allow the reliable prediction of ploidy level from morphology.

3c. ASTER PATENS Ait. var. PATENTISSIMUS (Lindl.) T. & G., Fl. N. Amer. 2: 115. 1841.

Aster patentissimus Lindl. in DC. Prod. 5: 232. 1836. Basionym.
Aster arnottii Nees ex T. & G., Fl. N. Amer. 2: 115. 1841, *pro. syn.* TYPE: Missouri. St. Louis, *Drummond* (possible ISOTYPES: K!).
Aster continuus Small, Bull. Torrey Bot. Club 25: 620. 1898. TYPE: ARKANSAS. Miller Co.: Texarkana, Aug 1898, *Heller* 4283 (HOLOTYPE: NY!).
Aster subsessilis Burgess in Small, Fl. SE. U. S., 1220. 1903. TYPE: ARKANSAS. Benton Co.: 1899, *Plank* (LECTOTYPE here designated: NY!; ISOELECTOTYPES (3): NY!).
Virgulus patens (Ait.) Reveal & Kenner var. *patentissimus* (Lindl. in DC.) Reveal & Keener, Taxon 30: 650. 1981.

Plants differing from the typical variety only in involucral features. Involucre more turbinate, usually over 8 mm tall (up to 12 mm), with phyllaries sometimes conspicuously decurrent on the peduncles, and ranging in number up to 50 or even 60, in 5–7 series, appressed; middle phyllaries

Figure 13. Lectotype of *Aster patens* Ait. var. *gracilis* Hook.

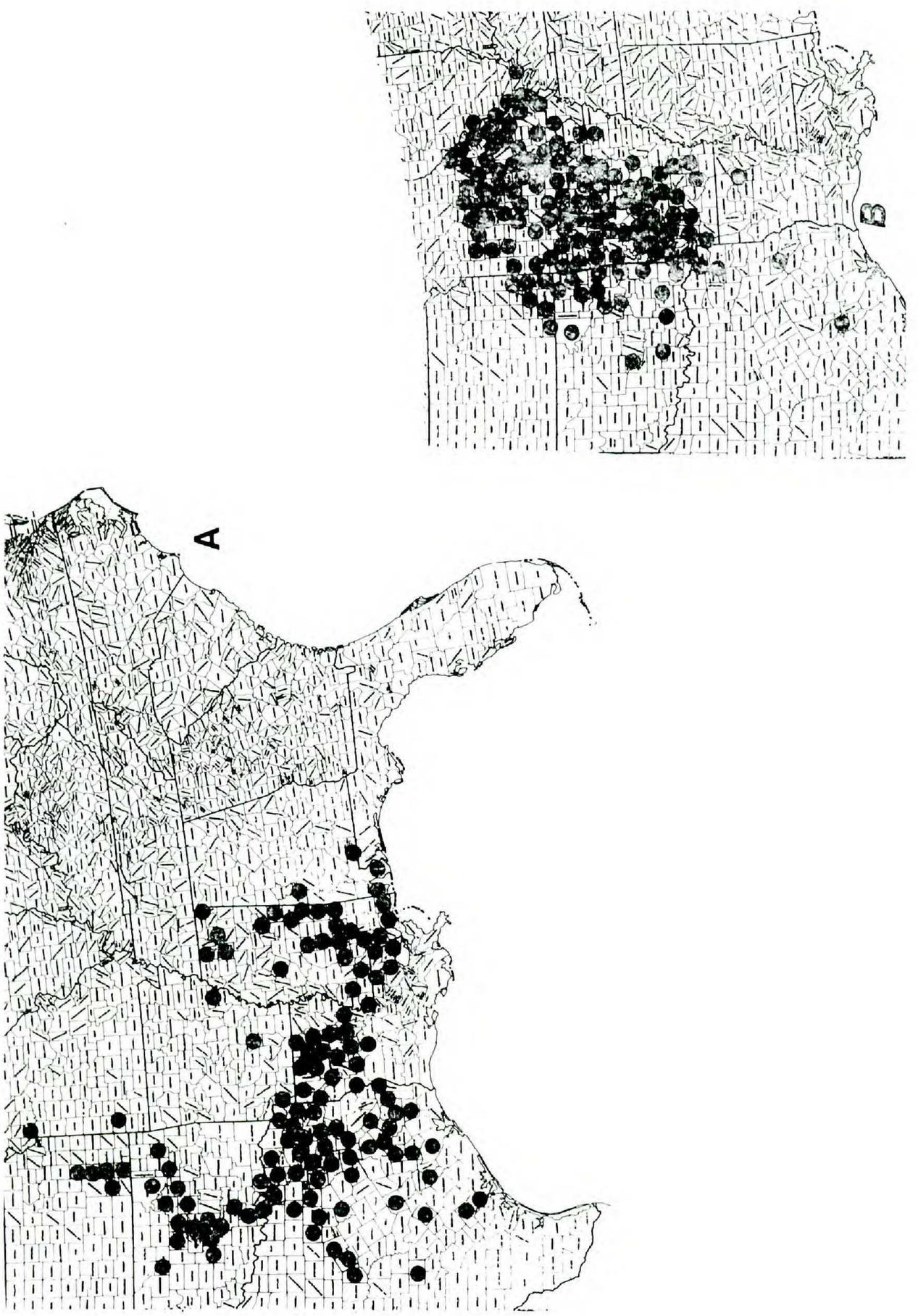

Figure 14. Map A. Distribution of *Aster patens* var. *gracilis*. Map B. Distribution of *Aster patens* var. *patentissimus*.

broadly linear, 4–6 mm long and 1.2–1.7 mm wide, broadly obtuse, ciliate to fimbriate, the indument predominantly strigillose, often canescent, glandular trichomes sometimes present but few and inconspicuous at 30×. $2n=20$, some with 1–4 B-chromosomes. Figure 15.

Distribution (Figure 14). Dry oak-pine and oak-hickory woodlands of the Interior Highlands and adjacent regions. Late August to early November.

TYPE: MISSOURI. St. Louis, 1831, *Drummond* (HOLOTYPE: CGE!).

Originally described as a species, this taxon was reduced to a variety by Torrey and Gray (1841), who noted that the involucral features "pass insensibly into the ordinary state of the plant." Although Gray (1884) later rejected the name even as a variety, most later authors have followed the original Torrey and Gray interpretation. Because there is a good relationship between genetically-based involucral features and geographic range, and also a number of plants with intermediate morphologies, I also treat this taxon at the varietal level.

Populations of *A. patens* var. *patentissimus* are found primarily in the uplands west of the Mississippi River and south of the Missouri River, in habitats similar to those occupied by the var. *patens* in the eastern range of the species. The most extreme forms of var. *patentissimus* occur in the higher elevations of the Ozarkian Plateau and Ouachitan Mountains. Populations of more intermediate morphologies are found throughout the Interior Highlands, but are most common in transitional regions such as southern Illinois, northeastern Texas, and eastern Oklahoma and Kansas.

EXCLUDED TAXA

ASTER FONTINALIS Alexander in Small, Man. Fl. SE. U. S., 1381. 1933 = *Aster patens* Ait. var. *floridanus* Long, Rhodora 72: 40. 1970. This taxon is a plant of southern Florida, possibly a good species, and allied with *Aster dumosus* L.

The sectional affinities of the following taxa need clarification, but they are not obviously allied with *Aster patens* Ait., and I have excluded them from the section *Patentes*: *Aster adnatus* Nutt., *Aster bimater* Standley & Steyermark, *Aster lima* Lindl. in DC., *Aster lucayanus* Britton, *Aster moranensis* H.B.K., and *Aster walteri* Alexander in Small.

ACKNOWLEDGMENTS

This paper is based on my doctoral dissertation deposited at Vanderbilt University, Nashville, Tennessee. I am especially indebted to Dr. Robert Kral for his direction and assistance during the course of the study. I thank Dr. Dean Whittier, Dr. Frederick T. Wolf, Dr. William Clement, and Dr. Giovanni DiSabato for their suggestions and advice. I am also grateful to Dr. R. B. Channell for his encouragement and helpful criticisms. During

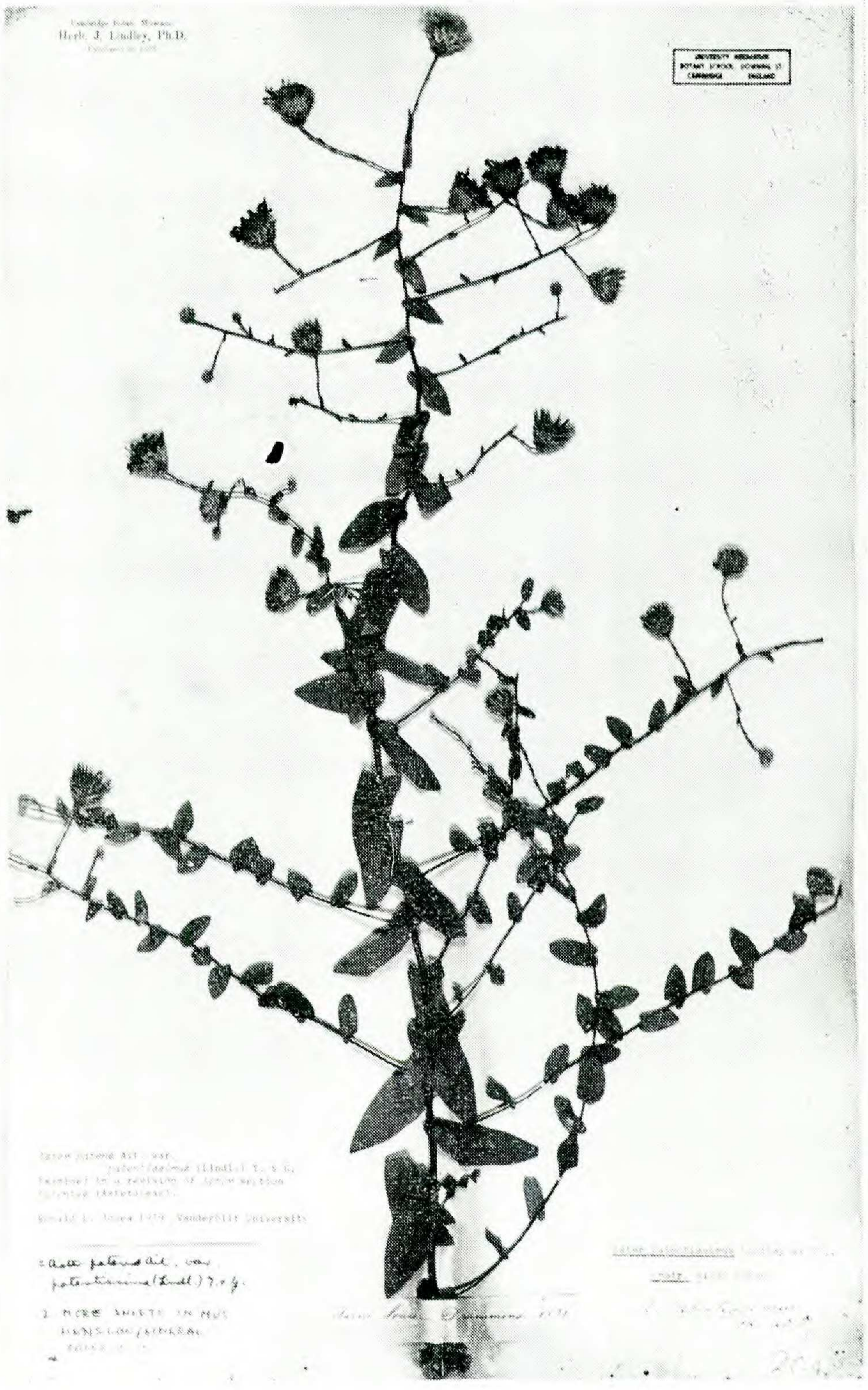

Figure 15. Holotype of *Aster patentissimus* Lindl. in DC.

my graduate work I received financial support through teaching and research assistantships from the Department of General Biology.

Significant contributions to this study have been made by the following botanists: Prof. William T. Stearn (BM) and Dr. Alicia Lourteig (P) kindly supplied information on types and gave counsel on other historical matters; and Dr. Arthur Cronquist (NY), Dr. Almut G. Jones (ILL), and Dr. John Semple (WAT) made available to me their ideas and information on the genus *Aster*.

I am grateful to herbarium curators who provided loans of specimens and other documentary materials. The following is a complete list of lending herbaria, identified by their acronyms according to Holmgren and Keuken (1974); ALU, B, BM, CGE, DUKE, F, FSU, GA, GH, IND, K, KANU, KY, LL, MICH, MIN, MO, NCU, NLU, NY, OKL, OS, P, PENN, PH, SMU, TENN, TEX, UARK, UNA, VDB, and WVA.

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